

EUROPEAN HEATHLANDS¹

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INTRODUCTION

Heathlands have long played a prominent part in the West European scene. From early times the languages of countries on the Atlantic fringe of the Continent contained words to describe them, notably "bruyère" (Romance origin), "lande" (Celtic origin) and "Heide" or "heath" (Gothic origin). Elsewhere in Europe related vegetation types were to be found on mountains, but in this western region from Scandinavia southwards to northern Spain (Fig. 14.1) heathlands were extensive also in the lowlands and played an important

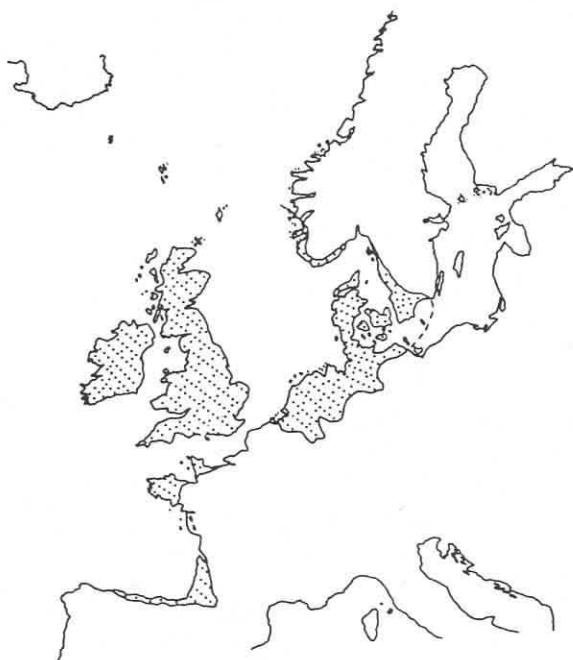


Fig. 14.1. Map showing the lowland heathland region of Western Europe.

part in the lives of people. As a result, the heathland landscapes of Europe (Fig. 14.2, 14.3) have caught the attention of painters, poets and writers as well as scientists, and have led to the evolution of unique patterns of land use, with their special traditions and tools. It was to this open, largely tree-less country on acid soils of low fertility, so often dominated by heather (*Calluna vulgaris*), that the word "heath" was first applied; though now as the name of a formation, "heathland" refers to vegetation of similar physiognomy throughout the world.

For many years, however, there was controversy about the origins and status of European heathlands. There has also been continuing argument about the ecological consequences of a long history of use for grazing, associated in some parts with regular burning as a means of vegetation management. This system of land use has resulted in ecosystems which are of particular interest because they are composed of naturally occurring, not cultivated, species and are systematically managed for herbivore production. This, together with the intrinsic interest of heathlands from the viewpoints of plant sociology, physiological ecology and community dynamics, has placed them amongst the most intensively studied ecosystems in Europe. It is the intention of this chapter, while providing a general account of European heathlands, to reflect the results of some aspects of these studies.

In recent years there has been a further development, namely a widespread and rapid decline, throughout much of Western Europe, in the area occupied by heathland vegetation. Increasingly, heathlands have gone out of production as grazing

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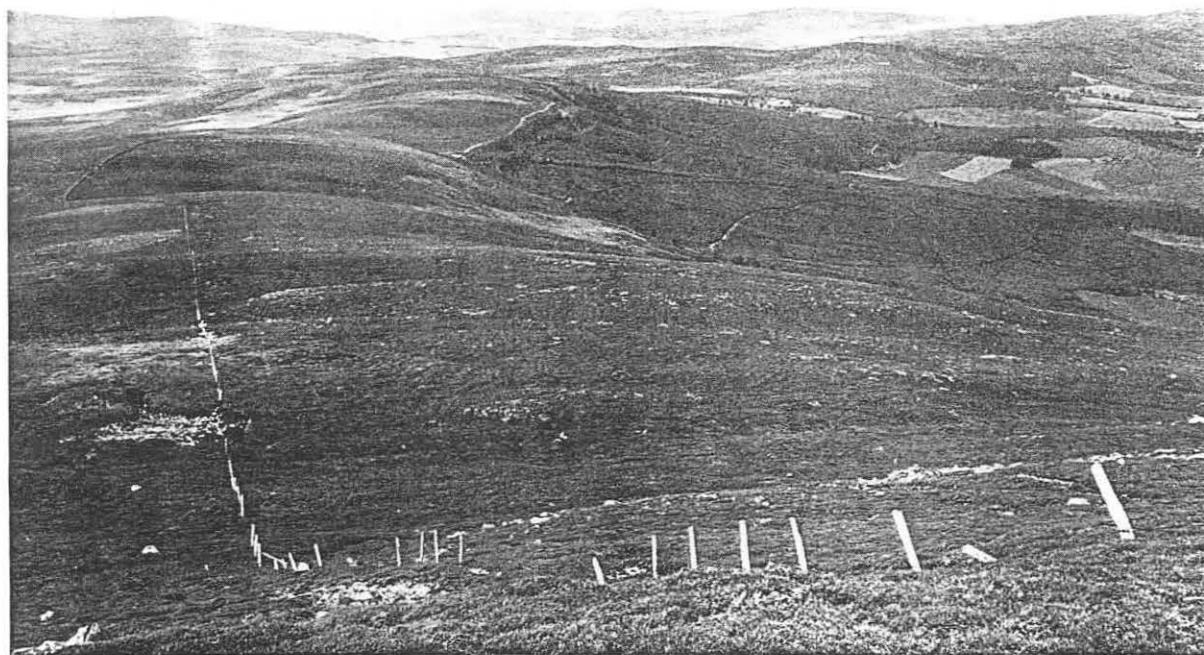


Fig. 14.2. Heathland landscape in Western Europe. Heath vegetation in northwestern Scotland, largely dominated by *Calluna vulgaris*. (Photo C.H. Gimingham.)



Fig. 14.3. Heathland with scattered tall shrubs (*Calluna vulgaris* with *Juniperus communis*). Lüneburger Heath, northern Germany. (Photo C.H. Gimingham.)

lands, and the traditional combination of low productivity with minimal inputs is being replaced by more intensive use for agriculture or forestry. While in this way soil improvement and enhanced production may be achieved, a distinctive type of landscape of great scientific, recreational and aesthetic value is in danger of extinction. This can be prevented only by an effective policy for the conservation of examples of the entire range of heathland communities throughout Western Europe. The results of research on heathland ecosystems must now be applied to the development of systems of management for nature conservation.

COMMUNITY STRUCTURE

Most European heathlands may be described as low (canopy at 1 m or less above ground) or dwarf (25 cm or less) heathland, with ericoid shrubs generally forming dense cover. As in other regions, they may conveniently be divided into three categories according to broad differences in habitat:

- (1) dry-heathlands
- (2) wet-heathlands
- (3) mountain and arctic heathlands

The first two belong to the lowland, temperate parts.

European heathlands

(1) Dry-heathlands

The community structure most commonly equated with heathland is best expressed in the dry-heathlands, developed on freely drained, nutrient-poor substrata where, for any reason, trees are very sparse or lacking (Fig. 14.2). Where tall shrubs such as *Juniperus communis*, *Ulex europaeus* or *Savothamnus scoparius* are present, though sparse, a tall open shrubland with heath is frequent, as in parts of southwestern Sweden, Denmark, The Netherlands, northern Germany (Fig. 14.3) and France. However, in the majority of heathlands neither trees nor tall shrubs contribute significant cover, leaving ericaceous species to form a dense stratum, less than 1 m in height, usually to the exclusion of all other life forms at this level (Fig. 14.4A). *Calluna vulgaris*, being a vigorous and

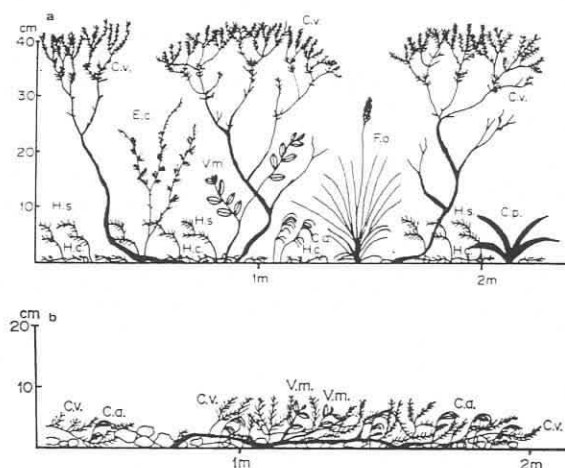


Fig. 14.4. Profile diagrams illustrating the structure of: A. *Calluna vulgaris*-dominated dry-heathland with *Erica cinerea* and *Vaccinium myrtillus*. B. Mountain dwarf heathland (*Calluna vulgaris* and *Vaccinium myrtillus*).

Legend: C.a. = *Cladonia arbuscula*; C.p. = *Carex pilulifera*; C.v. = *Calluna vulgaris*; E.c. = *Erica cinerea*; F.o. = *Festuca ovina*; H.c. = *Hypnum cupressiforme*; H.s. = *Hylocomium splendens*; V.m. = *Vaccinium myrtillus*.

relatively long-lived species (see p. 387) which includes the whole of the West European heathland region within the limits of its distribution (Fig. 14.5), is a widespread dominant. While this plant is sometimes associated with other Ericaceae of similar stature, (e.g. *Erica cinerea*, *Vaccinium myrtillus*), it is replaced as dominant only in habitats at the margins or beyond the limits of its ecological range.

Below this low-shrub canopy there may be a discontinuous stratum of partially shade-tolerant, often creeping dwarf shrubs [e.g. *Vaccinium vitis-idaea* (Fig. 14.6), *Empetrum nigrum*, *Arctostaphylos uva-ursi*] with some herbs and graminoid plants, reaching to about 20 cm above the surface. Robust bryophytes (e.g. *Pleurozium schreberi*) and a few rosette or creeping vascular plants may form another layer at 5 to 10 cm, while smaller bryophytes or lichens constitute a ground stratum. The extent to which these subordinate strata are developed and their density depend both on the habitat and on the age structure of the stand of the dominant species (Gimingham, 1972).

(2) Wet-heathlands

In acid oligotrophic habitats, wet-heathland occurs on soils with impeded drainage or on



Fig. 14.5. Map of the main area of distribution of *Calluna vulgaris*; outlying stations omitted.
 Legend: - - - - - , approximate limits of distribution; - · - · - · - , area within which *Calluna* is commonly a community dominant;
 — , approximate area of ecologically optimal habitats. (After Beijerinck, 1940, modified.)

continually moist organic substrata. These communities occupy an intermediate position on the vegetational gradient from dry-heathland to mires on saturated peat; the wet end of this sequence is covered in Volume 4 of this series. Trees are seldom present on wet-heathlands in the more oceanic parts of the region, though elsewhere they may occur sparsely. Tall shrubs, represented commonly by *Salix* species, are sometimes present as isolated individuals or in small clumps, and the low shrubs are normally less dense than in dry-heathlands.

In habitats of moderate moisture status, where the surface at least is aerated for part of the summer, a type sometimes described as "humid heath" occurs, in which *Calluna vulgaris* is mixed with *Erica tetralix*, and while grass and sedge

species are abundant there is little *Sphagnum* moss. In the wet-heathlands on permanently moist soils, the contribution of *Calluna* is much reduced and often confined to hummocks (Rutter, 1955). Its place is increasingly taken by other ericaceous shrubs such as *Erica tetralix* or *Ledum palustre*, and by *Myrica gale* on very wet peat. These shrubs generally produce an open-heathland, with considerable admixture of tall grass such as *Molinia caerulea* or tufted sedges (e.g. *Eriophorum* sp., *Trichophorum caespitosum*). There is normally a dense ground stratum composed chiefly of *Sphagnum* species, associated with various other bryophytes and small herbs. Lichens are largely absent.



Fig. 14.6. *Vaccinium vitis-idaea*, occupying the centre of a degenerate *Calluna vulgaris* bush (northeastern Scotland). (Photo C.H. Gimingham.)

(3) Mountain and arctic heathlands

Under the more extreme climatic conditions beyond the normal altitudinal and latitudinal limits of forest, dwarf heathland is widespread. Here dwarf shrubs (Ericaceae, *Salix* spp. etc.) form a low mat, often no more than 10 cm in height (Fig. 14.4B), of entwined stems and branches, sometimes dense and continuous but often restricted to stripes or patches. Graminoid species and a variety of bryophytes and lichens contribute to the community. Vegetation of similar structure occurs in exposed coastal localities. The arctic heathlands are covered more fully by Bliss in Chapter 15.

Life forms

The range of life forms represented in a typical dry-heathland is indicated by the examples given in Table 14.1. The predominant category is that of the low shrub with very small (leptophyll), evergreen, sclerophyllous, more or less cylindrical leaves, such

as *Calluna vulgaris* (Fig. 14.7), *Erica* spp., and *Empetrum* spp., all of which can behave as dwarf shrubs (< 25 cm) as well. In addition, there are low or dwarf shrubs with flat, sclerophyllous leaves in the nanophyll (or bordering on microphyll) category, such as *Vaccinium vitis-idaea* (Fig. 14.6) and *Arctostaphylos uva-ursi*. These examples are evergreen, but some are deciduous, or largely deciduous (retaining only some of the youngest leaves in winter) such as *Vaccinium myrtillus*, *Arctous alpinus*, and non-ericaceous plants such as *Salix repens* (Salicaceae), *Myrica gale* (Myricaceae) and *Genista anglica* (Fabaceae). The latter, like the species of *Ulex* which belong to heathland communities [*U. europaeus*, *U. gallii* and *U. minor* (Fig. 14.13)], possesses spines, but otherwise spines are not characteristic of European heathland species.

Among the hemicryptophytes, graminoid herbs (both caespitose and rhizomatous) are generally represented, many being evergreen but a few deciduous. Some heathland communities occupy-

TABLE 14.1

Analysis of life-forms of vascular plant species in three examples of West European heathland communities (numbers of species in each class)

	Dinnet Muir, Aberdeenshire, NE Scotland Herb-rich <i>Calluna</i> - <i>Arctostaphylos</i> heathland	Mästocka, Halland, SW Sweden <i>Calluna</i> - <i>Vaccinium</i> - <i>Arctostaphylos</i> heathland	Wilsede Berg, Lüneburger Heath, N Germany <i>Calluna</i> - <i>Genista</i> heathland
PHANEROPHYTES			
Small trees (2–10 m)	1	2	1
Low shrubs (25–100 cm)	2	1	1
CHAMAEPHYTES			
Creeping dwarf shrubs, stems often intertwined to form mats	1	4	1
Dwarf shrubs with erect or ascending stems (< 25 cm)	2	3	3
HEMICRYPTOPHYTES			
(1) Graminoid herbs			
(a) Caespitose, tillering herbs, evergreen	5	3	3
(b) Sparingly tufted, more or less rhizomatous, evergreen	1	1	0
(2) Forbs			
(a) with erect or scrambling stems, dying back in winter	5	2	0
(b) seasonal rosettes	1	3	0
(c) creeping	1	1	0
(d) evergreen	3	1	0
HETEROTROPHIC			
Twining parasites	0	0	1
Total number of species	22	21	10

ing soils of at least moderate nutrient status are described as "herb-rich", indicating the presence of a fair number of forbs as well as graminoids, ranging from creeping and scrambling types to rosettes, both evergreen and seasonal. Geophytes, mostly dying back in winter to underground tubers or rhizomes, are also represented. Annuals are extremely few.

A few species of heathland communities are partial root parasites (e.g. *Melampyrum pratense*, *Pedicularis sylvatica*), and a twining vascular parasite (*Cuscuta epithymum*) is widespread, except in northern heathlands. Many European heathlands are noteworthy for their rich flora of either bryophytes or lichens. About 75% of the total number of species of green plants recorded in dry-

heathlands are bryophytes or lichens; an even greater percentage has been recorded in wet-heathlands (Table 14.2). Agaric fungi are also numerous.

Relationships with other types

The communities of dry-heathlands are floristically closely related to those of tall scrub and woodlands on similar soils, including woods with *Picea abies*, *Pinus sylvestris*, *Quercus* species, and *Fagus sylvatica*. To the south of the heathland region they merge into Mediterranean scrub types, where, apart from tall species of *Erica*, the communities are generally characterised by taller shrubs with larger leaves. There is also a close



Fig. 14.7. Twig of *Calluna vulgaris* (natural size), showing two complete annual increments. (Photo E. Middleton.)

relationship to grassland, which in the absence of trees may take the place of heathland under heavy grazing, or on soils of higher nutrient status, or with increasing continentality of climate.

Wet-heathlands link closely with the vegetation of acid mires (see Volume 4 of this series), for the shrubs give place to Poaceae (*Molinia caerulea*, *Nardus stricta*) or Cyperaceae (*Eriophorum* spp., *Trichophorum caespitosum*) under conditions which encourage active peat formation. This transition may also be promoted by grazing and burning.

Dwarf heathland is characteristic of the low-alpine zone on European mountains (or low- and middle-alpine in the more oceanic parts; McVean and Ratcliffe, 1962). Under still more severe conditions it is replaced by bryophyte- or lichen-dominated vegetation, or by discontinuous "fell-

field" communities. Similarly, in the north, tundra heathlands give place to grass-sedge tundra, lichen tundra or moss tundra.

Root systems

On podzols, as well as on poorly aerated organic soils, heathland vegetation is shallow-rooting. The bulk of the finely branched root system of *Calluna vulgaris* (much of which is derived adventitiously from buried stems) is usually confined to the upper 20 cm of the soil profile (Chapman, 1970). A limited number of roots may penetrate more deeply, especially on freely drained, sandy soils, but where either a hard pan or a waterlogged layer is encountered they may form an intertwined mat at this level (Gimingham, 1972).

Many of the other species also root predominantly in the upper 20 cm (e.g. *Erica cinerea*, *E. tetralix*, *Ulex minor*, *Agrostis* spp., *Festuca* spp.), but some extend to lower levels especially in sandy or gravelly soils (e.g. *Deschampsia flexuosa*, *Carex arenaria*) and in the deeper peats (e.g. *Molinia caerulea*, *Eriophorum* spp., *Trichophorum caespitosum*, all of which may extend to 60 cm or more).

Many heathland species, though not *Calluna vulgaris*, are rhizomatous [e.g. *Erica tetralix*, *Vaccinium myrtillus*, (Fig. 14.8)]. Others have tuberous perennating organs (*Potentilla erecta*, *Listera cordata*). The majority of the shrubs are mycotrophic, while *Myrica gale* and species such as *Genista* spp., *Ulex* spp. and *Lathyrus montanus* (Fabaceae) have nitrogen-fixing root nodules.

ECOLOGICAL DISTRIBUTION

Climate

The area of Western Europe indicated in Fig. 14.1 may be termed the "heathland region" for it is here that heathland vegetation occupies extensive tracts of lowland, whereas elsewhere it is confined to upland habitats. The climate of this region belongs to Köppen's (1923) **Cfb** category, which indicates moist, temperate conditions with mild winters and relatively long spring and autumn periods (Table 14.3). The mean temperature of the warmest month is normally less than 22°C, while at least four months have means above 10°C.

TABLE 14.2

Species-area data (mean number of species per quadrat) for five British Heathlands (after Hopkins, 1955 and pers. comm., 1978)

Locality	Species-area data	Quadrat size (m ²)							
		0.01	0.25	1	4	16	25	100	400
Matley heathland	all species	8.6	16.7	18.2	22.1	25.0	25.7	28.0	34.0
	angiosperms	3.9	6.4	6.7	7.4	8.2	8.4	9.5	12.0
Shropshire heathland	all species	6.4	11.9	13.2	16.2	20.0	20.8	25.0	32.0
	angiosperms	1.8	2.6	3.2	3.7	4.6	5.0	6.3	8.0
Yorkshire heathland	all species	1.6	2.7	4.7	8.0	12.9	14.1	20.3	24.0
	exl. lichens								
Pennine bog-heathland	angiosperms	1.1	1.4	1.9	2.4	3.6	3.6	5.3	7.0
	all species	6.7	14.3	17.0	26.1	33.8	35.3	41.3	46.0
Perthshire bog-heathland	angiosperms	2.1	2.8	3.3	4.3	5.4	5.6	6.3	7.0
	all species	9.6	17.5	19.5	23.7	27.7	29.5	35.8	48.0
	angiosperms	3.5	5.5	6.3	6.8	7.4	7.5	8.5	10.0

Matley heathland, 3.2 km east of Lyndhurst in the New Forest — dominated by *Calluna vulgaris*, *Erica tetralix* and *Molinia caerulea*. Total number of species present: 12 angiosperms, 11 bryophytes, and 11 lichens.

Shropshire heathland, on Long Mynd about 3.2 km southwest of Church Stretton — dominated by *Calluna vulgaris*, burnt about five years before the site was sampled. Total number of species present: 8 angiosperms, 11 bryophytes, and 13 lichens.

Yorkshire heathland, about 13 km west of Richmond — dominated by *Calluna vulgaris*, not burnt for seven to twelve years before sampling. Total number of species present: 7 angiosperms, 17 bryophytes and more than 9 lichens.

Pennine bog-heathland, Moor House National Nature Reserve, about 14.5 km south of Alston — part of a blanket bog at an altitude of 550 m with *Calluna vulgaris*, *Eriophorum vaginatum* and several species of *Sphagnum* frequent. Total number of species present: 7 angiosperms, 7 *Sphagnum* spp., 20 other bryophytes, and 12 lichens.

Perthshire bog-heathland, near Rannoch station, on an area of bog at an altitude of 290 m, burnt a few years before it was sampled. The most frequent species were *Calluna vulgaris*, *Erica tetralix*, *Narthecium ossifragum*, *Trichophorum caespitosum*, *Eriophorum angustifolium*, several species of *Sphagnum*, several liverworts and the lichens *Cladonia impexa* and *C. uncialis*. Total number of species present: 10 angiosperms, 7 *Sphagnum* spp., 17 other bryophytes, and 14 lichens.

However, heathlands occur only in the more strongly oceanic parts of the Cfb zone, where the annual rainfall is relatively high and well spread throughout the year (c. 600 to 1100 mm, falling on more than 115 rain days per year). Heathlands are, however, best developed under conditions intermediate between those of subcontinental régimes and those described as “hyper-oceanic”, which are experienced in the extreme west of southern Norway, in parts of northwest Scotland and in west Ireland, where except on the steeper slopes peatlands are more characteristic than heathlands.

Many of the ericaceous shrubs and other species typical of European heathlands show more or less pronounced oceanic affinities in their geographical distribution, notably *Erica cinerea*, *E. tetralix*, and to a lesser extent *Calluna vulgaris* and *Vaccinium myrtillus*. Bannister (1970) interprets this as a requirement for mild winters, based (at least in the first two species mentioned above) on susceptibility

to winter drought. Certainly mild winters, as well as the absence of extended periods of high evaporation stress in summer, characterise the region in which these plants are among the dominants of heathland vegetation.

The climatic conditions under which dwarf heathland develops on European mountains are, typically, those of the low-alpine zone (c. 1200 to 1500 m). In the more oceanic parts, however, as in Britain, persistent cloud and mist, low summer temperatures and a short growing season all combine to confine the dwarf heathlands to lower altitudes, for instance from 360 to 850 m in northern Scotland (Poore and McVean, 1957). Both here and in the arctic, heaths are tolerant of high levels of exposure to wind, but tend to be eliminated where wind prevents the formation of a protective snow cover in winter. On the other hand, heath communities do not survive late snow lie and are not found under snow patches.

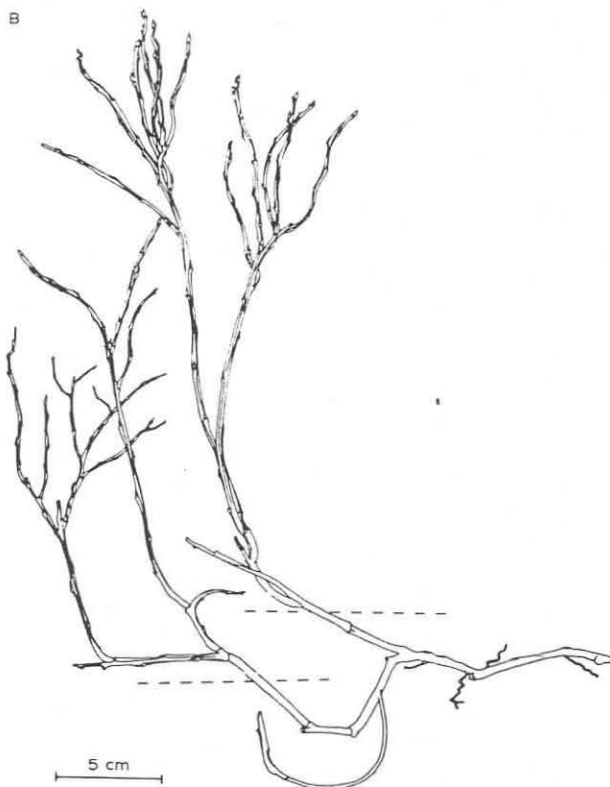
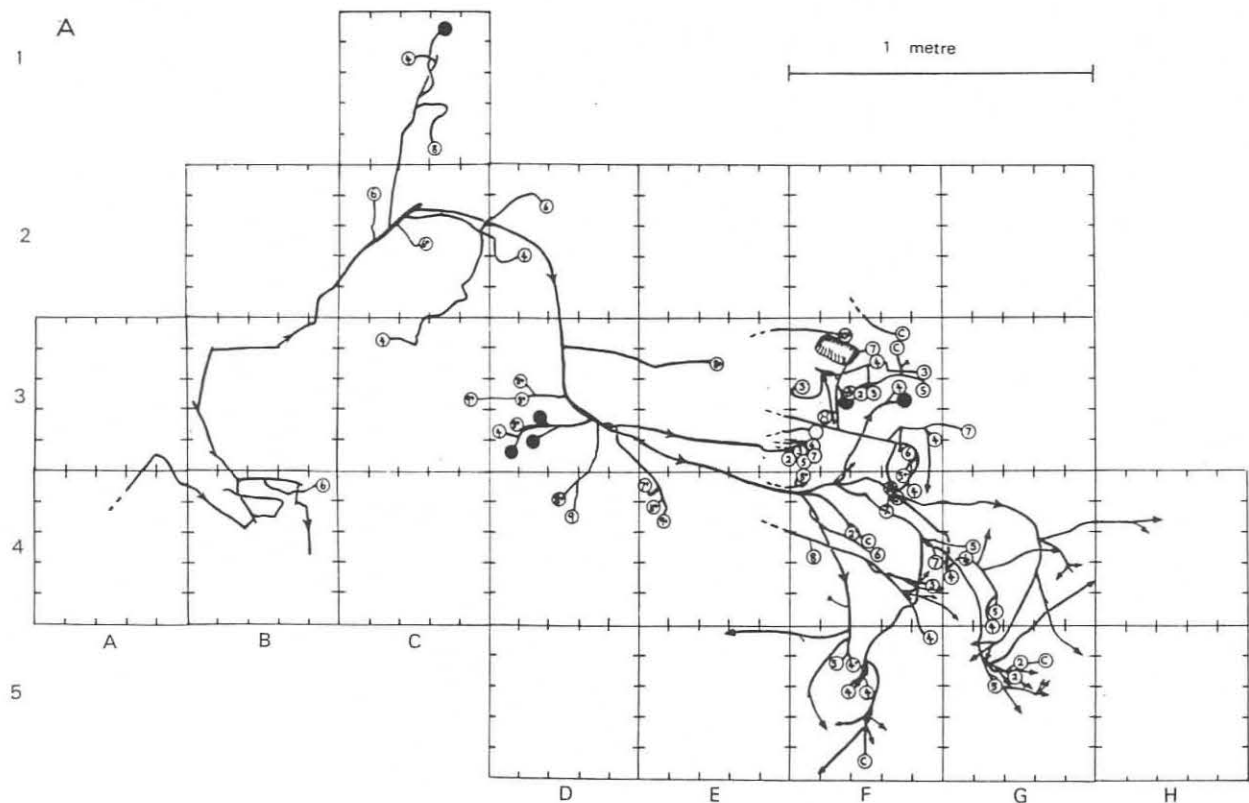


Fig. 14.8. *Vaccinium myrtillus*. A. Excavated rhizome system *in situ*. Open circles with figures give the age in years of living branches, closed circles are dead branches of unknown age. B. Rhizome and shoot system (winter condition). (Figure from Flower-Ellis, 1971.)

Soils

As in other parts of the world, European heathlands generally belong to acid substrata of low nutrient status. These include stabilised siliceous sand, various types of podzolic soils derived from freely drained parent materials including fluvio-glacial sands and gravels, glacial tills and weathered rock debris, oligotrophic brown earth soils, humic gleys, ranker soils and peat (Table 14.4). With some exceptions, heathlands are absent from soils rich in exchangeable nutrients, especially calcium.

The freely drained substrata give rise to dry-heathlands, which are generally associated with podzolic soil profiles. *Calluna vulgaris* and its associated ericaceous shrub species produce abundant litter, rich in polyphenols, which is relatively

TABLE 14.3

Climatic means from selected localities in the lowland heathland region of Western Europe

	Locality	Mean temperature (°C)		Rainfall mean for year (cm)	Rain days mean for year	Mean relative humidity at mid- day in the driest month (‰)
		January	July			
Norway:	Stavanger	1.4	15.3	108.5	153 ¹	64 (May)
Sweden:	Simlångsdalen	-1.4	17.0	103.6	—	—
Denmark:	Studsgaard	-0.6	16.1	79.0	133 ¹	62 (May)
	Aarhus	-0.6	16.7	67.6	117 ¹	59 (May)
Great Britain:	Aberdeen	3.0	14.2	83.8	199 ²	70 (June)
	York	3.6	16.7	62.7	179 ²	76 (June)
	Plymouth	6.4	15.8	96.0	183 ²	72 (April, May)
Netherlands:	Groningen	1.4	17.5	74.7	203 ³	59 (May)
Germany:	Lüneburg	0.0	17.2	61.2	123 ¹	55 (May)
France:	Caen	4.7	17.2	68.1	155 ³	—
	Bordeaux	5.3	20.6	82.1	164 ³	54 (August)
Spain:	Santander	9.2	19.2	112.0	177 ³	71 (March)

The definition of "rain days" varies from country to country. Suffixes indicate bases of calculation as follows: ¹ days with 0.1 cm rain, or more; ² days with 0.025 cm rain, or more; ³ days with 0.01 cm rain, or more.

Table extracted from Gimingham (1972) where references are given to primary sources of data.

slow to decompose and forms an accumulation of acid raw humus (*mor*) on the soil surface. This is avoided by deep-burrowing earthworms and consequently is not readily mixed with the mineral material. However, humic acids are taken up as water drains downwards following the frequent falls of rain, and iron, aluminium and other ions are mobilised and transported to lower levels. According to the proportions in which these are deposited in the B horizon, the soils may be described as iron podzols, humus podzols or iron-humus podzols. In heath podzols considerable amounts of humic material may be seen in the A horizon, sometimes forming a distinct A₁, at others staining the whole eluvial horizon. The formation of a hard pan in the B horizon is also a common feature of heathland podzols: this may be a humus pan as in the deep podzols of the northern German or Danish plains, or a thin iron pan as in many British moorland soils.

Heathlands may also develop on oligotrophic brown earths (Coombe and Frost, 1956), but the dominance of *Calluna vulgaris* seems always to lead to acidification (Grubb et al., 1969) and eventual podzolisation. Dumbleby (1952, 1962) has presented evidence from Yorkshire, northern England, of the conversion of brown-earth soils to podzols as a result of replacement of deciduous

forest by heathland in Bronze Age times (c. 1000 B.C.). Even certain eutrophic brown soils or calcium-rich substrata such as limestone or chalk soils may sometimes bear heathland, presumably when surface leaching has been sufficiently pronounced to permit the establishment of heathland species. "Chalk heath" is a well-known community including both calcicolous and heathland species (Grubb et al., 1969).

Acid soils with impeded drainage lead often to the development of wet-heathland, which is associated with the formation of thick layers of peaty humus. This type of heathland is also found at the margins of peat bogs and on wet hillsides in high-rainfall areas. Actively growing, deep saturated peat is beyond the ecological range of heathland vegetation, but where peat deposits have begun to dry out or have been subject to artificial drainage, so that the surface is aerated at least in summer, the original bog community may be replaced either by wet-heathland, or where surface drying is advanced, by luxuriant *Calluna vulgaris* heathland.

The soils of mountain or arctic dwarf heathland are usually rankers¹ and tundra rankers.

¹ A ranker is defined by Kübiena (1953) as a "soil formation low in lime, whose humus horizon lies immediately on the parent material, which consists usually of lime-deficient siliceous or silicate rocks".

In the majority of heathland soils pH lies in the range between 3.4 and 6.5 and the C/N ratio is high. The soils generally show relatively low levels of exchangeable cations, and are almost invariably described as deficient in phosphorus (Table 14.4). Application of phosphatic fertiliser leads to increase in the concentration of phosphorus in the vegetation, and in most ericaceous species to a marked improvement in flowering. The soils also frequently appear to be nitrogen-deficient, since addition of nitrogen fertiliser leads to increased shoot growth in many species, but this is presumably an expression of low rates of mineralisation of nitrogen rather than any deficiency in total nitrogen content.

ORIGINS AND STATUS

The climatic and edaphic environment of the lowland heathlands of Western Europe, described above, is clearly one which could, in most instances, equally well support forest. Indeed, remnants of "natural" forest are to be found side by side with heathland: boreal coniferous forest in the

northern part of the heathland region (Norway, parts of Sweden and Scotland), and oakwood (*Quercus* spp.) or beechwood (*Fagus sylvatica*) to the south. Furthermore, examples of heathlands being invaded by trees are common (Fig. 14.9). The explanation of the origins of heathlands therefore becomes the explanation of the lack of trees.

In the case of mountain dwarf heathlands, tundra heathlands and certain heathland communities of exposed coastal sites this may be attributed to severe climatic conditions. Other heathlands are seral, for example dune heathlands and those on drying peat surfaces (pp. 386–387), and owe their existence to successional processes which, in the absence of any deflecting factor, would be expected to continue towards the development of woodland. Tansley (1939) even went so far as to suggest that some of the inland heathlands of southern England represent a stage in the post-glacial succession of vegetation, the further development of which was arrested by human intervention (burning and grazing).

In some instances, heathlands may be edaphically determined. This might apply to certain wet-



Fig. 14.9. Heathland invaded by *Betula pubescens*. Dinnet Muir, Scotland. (Photo C.H. Gimingham.)

TABLE 14.4

Soil analyses from examples of heathland on various types of substratum (Scotland)

Horizons		Sample depth (cm)	Soil separates			Organic fraction				Exchangeable cations (meq 100 g ⁻¹)						% Base saturation	Phosphorus mg P ₂ O ₅ 100 g ⁻¹		pH
			% sand	% silt	% clay	% C	% N	C/N	% OM	Ca	Mg	Na	K	H	Total		total	acetic soluble	
<i>I. Coastal dune heathland: Sands of Forvie, Aberdeenshire (altitude 15 m)</i>																			
A ₁	dark brown humic material with sand grains	2–6	80.3	1.4	4.8	8.89	0.25	35.6	15.3	1.35	0.69	0.39	0.54	20.4	23.37	12.7	66	3.0	4.20
A ₂	bleached layer: whitish grey sand	11–12	91.3	0.6	5.5	1.21	0.07	13.7	2.1	0.15	0.08	0.09	0.04	nil	0.36	100	30	2.0	4.80
B ₂	yellow orange stained sand	23–27	93.9	0.5	5.2	0.24	0.02	12.0	0.4	0.15	0.09	0.04	<0.005	nil	0.28	100	30	3.0	5.61
	gleyed boulder clay underlying the blown sand	40–44	64.9	10.8	21.1	2.98	0.15	19.9	5.1	3.60	0.97	0.30	0.25	10.0	15.12	33.4	71	1.6	6.05
<i>II. Podzol with thin iron pan: Cairn o' Mount, Kincardineshire (granite boulder clay) (altitude 380 m)</i>																			
H	black decomposed raw humus	18–23	n.d.	n.d.	n.d.	54.0	1.27	41.0	93.0	1.375	3.64	n.d.	0.232	44.3	49.55	10.6	150	1.39	4.17
A ₂	bleached loamy coarse sand	25–36	82.4	11.28	6.32	2.94	0.124	28.0	5.06	<0.15	<0.08	n.d.	0.019	5.5	5.52	0.35	80	0.98	4.39
A _{2g}	gleyed bleached layer	43–53	77.9	10.9	11.2	3.94	0.166	28.0	6.78	0.281	<0.08	n.d.	0.052	11.2	11.53	2.86	60	0.896	4.63
Iron Pan (0.2 cm)																			
B ₃	indurated layer	53–63	74.1	13.6	12.3	n.d.	n.d.	n.d.	n.d.	0.313	<0.08	n.d.	0.066	3.75	4.13	9.21	80	0.523	4.86
B ₃ /C	weakly indurated layer	79–91	86.6	7.1	6.3	n.d.	n.d.	n.d.	n.d.	0.132	<0.08	n.d.	0.051	1.56	1.74	10.4	80	0.612	4.83
C	loose parent material	102–117	84.5	7.95	7.55	n.d.	n.d.	n.d.	n.d.	1.91	<0.08	n.d.	0.064	1.71	3.68	53.5	70	0.613	4.86

III. Drained deep peat: Sourhope Farm, Roxburghshire (altitude c. 400 m)

0-10	-	-	-	59.50	1.520	39.2	86.9	4.95	9.19	0.52	1.25	109.74	125.65	12.7	167	14.2	3.39
10-20	-	-	-	57.40	1.540	37.2	98.8	2.48	8.20	1.08	0.75	114.27	126.78	9.8	127	10.6	3.35
20-30	-	-	-	58.70	1.378	42.6	101.0	2.86	10.89	1.19	0.42	130.00	145.36	10.6	98	5.5	3.40
41-51	-	-	-	63.00	1.520	41.4	109.0	1.79	11.24	1.10	0.19	133.40	147.72	9.6	69	1.7	3.50
61-71	-	-	-	61.40	1.169	52.5	106.0	1.07	9.65	1.09	0.14	128.90	140.85	8.1	57	0.9	3.56
91-102	-	-	-	50.40	1.551	32.4	86.9	<0.15	7.79	0.95	0.14	115.00	123.88	7.2	50	0.7	3.65
122-130	-	-	-	48.10	1.398	34.4	84.0	<0.15	1.32	0.42	0.09	117.80	119.63	1.5	67	-	4.00

IV. Mountain heathland on relatively freely drained sub-alpine soil: Morven, Aberdeenshire (meta-basic igneous till) (altitude 618 m)

black peaty humus, few bleached quartz grains	5-13	n.d.	n.d.	n.d.	17.47	1.061	16.5	30.01	1.31	0.91	0.22	0.30	64.44	67.18	4.1	379	1.9	4.30
dark brown mealy amorphous humus, many angular stones	18-25	n.d.	n.d.	n.d.	17.39	0.925	18.8	29.39	nil	0.20	0.14	0.20	48.18	48.72	1.1	552	1.0	4.82
dark reddish brown gritty loam	33-38	77.8	11.1	4.8	4.07	0.257	15.8	6.99	nil	0.04	0.07	0.05	14.90	15.06	1.1	477	4.4	4.89
brown stony and gritty sand loam	46-53	73.4	14.3	9.9	1.82	0.114	16.0	3.13	nil	0.29	0.10	0.08	3.33	3.80	12.4	430	36.7	5.00
brown stony firm sandy loam	69-76	64.7	23.2	9.1	2.90	0.138	21.0	4.98	nil	0.06	0.17	0.24	3.81	4.28	11.0	622	52.9	5.31

Analyses by Soil Survey of Scotland, Macaulay Institute for Soil Research.

I, II and III extracted from Gimingham (1960).

n.d. = not determined.

heathlands on very poorly drained organic substrata, but it is difficult to demonstrate that, given a suitable climatic régime, any soil capable of supporting wet-heathland could not support some type of woodland. It was claimed by Müller (1924) that the widespread dry-heathlands on the glacial outwash plains of Jutland, Denmark, owe their existence in large measure to failure of forest development due to the presence of indurated soil horizons dating from the late glacial tundra phase. However, this view has had to be revised in the light of more recent investigations.

Even as early as 1892 it was held by Krause that heathlands in northern Germany occupied areas formerly covered by forest, and this view was further developed by Graebner (1901). Shortly afterwards, Smith (1902, 1911) showed that Graebner's interpretation could be extended to Scotland, where the frequent presence of tree stumps, roots, branches and bark preserved in humus or peat beneath present-day heathland vegetation offered good evidence of its derivation from former woodland. Since then this hypothesis has been amply supported by evidence from pollen analysis in heathland areas in Norway (Faegri, 1940), Sweden (Malmström, 1937, 1939), Denmark (Iversen, 1941, 1949; Jonassen, 1950), The Netherlands (Waterbolk, 1957), France (Duchaufour, 1948, 1956) and Britain (Godwin, 1944a, 1948, 1956; Mitchell, 1951, 1956; Morrison, 1959; Dimbleby, 1962, 1965; Smith and Willis, 1962). In all these areas the former existence of forest is confirmed, and clear indication given of its decline and replacement by vegetation dominated by Ericaceae.

This still leaves the cause of the change unexplained. Graebner (1901) thought that the replacement of forest by heathland could be explained largely as a natural consequence of continued soil podzolisation in an Atlantic type of climate. Although recognising that the process had been greatly accelerated by human intervention, this amounts to a view of heathland as at least potentially a "climax" vegetation type. Faegri (1940) maintained that, at least in southwest Norway, the prime cause was climatic change towards increased oceanicity, occurring at the onset of the Subatlantic period. This, in his view, constituted a climatic predisposition towards change, which may have been actualised or accel-

ated by human interference. This explanation, as applied to the extreme north of the heathland region, has received support from Bøcher (1943) with reference to the Faerøerne Islands (Faeroes), and Durno (1958), whose diagrams for northern Scotland suggest that changes of this kind began before man is likely to have had a significant influence.

Under the milder climatic conditions of much of the region, however, it is difficult to account in this way for the widespread decline of forest and its replacement by heathland. Further, the evidence from pollen analysis establishes beyond doubt that this change was by no means synchronous throughout the region, and in numerous localities bore no particular relation to the onset of the Subatlantic period. Often, the vegetational change is associated with signs of human activity — charcoal layers, artefacts, and pollen of cereals, and grasses or agricultural weeds such as *Plantago lanceolata*. Instances of conversion from forest to heathland have now been found from as early as the late Neolithic period (c. 2500 B.C. onwards) in Denmark (Iversen, 1941, 1949), The Netherlands (Waterbolk, 1957) and southeast England (Godwin, 1944a, b). They become more frequent in Bronze Age times, and are very commonly associated with the start of the Iron Age following 500 B.C., which broadly coincided with the onset of the Subatlantic period. There are also many well-documented cases of later origin of heathlands, extending throughout the historical period up to late in the nineteenth century.

Although the coincidence of a period of increased human impact with a significant climatic shift makes it difficult to disentangle these potential causes, the evidence for ascribing the origins of heathlands very largely to human influence, throughout the greater part of the region, is now overwhelming. Pollen analysis has revealed the details of the first temporary inroads into the forest, known by the Danish term *landnam*, which widely preceded more permanent clearance. Landnam is heralded by a decline in the values for total tree pollen, often associated with charcoal deposits indicating the use of fire. This is immediately followed by evidence of a phase of agriculture (pollen of cereals and weeds of cultivation); then by an increase in the pollen of Ericaceae and Poaceae signifying a temporary

stage of heathland or grassland prior to return of woodland as the area was abandoned. This sequence of events may be repeated several times, representing successive periods of occupation, before a more lasting retreat of the forest is shown. In heathland areas this is accompanied by a massive and persistent rise in ericaceous pollen.

Landnam sequences clearly demonstrate the ability of trees to recolonise once an area was abandoned. Any lasting replacement of forest by heathland therefore implies continued use of the land by man and the maintenance of some form of management. It was, in fact, because the open areas, whether heathland or grassland, were found to be valuable for the increasing stocks of domestic herbivores (mainly cattle and sheep) that they were retained in this form by grazing management supplemented, as necessary, by burning.

At first, only a small proportion of the extensive forest cover of Europe was destroyed to make way for heath or grassland, mainly in coastal and lowland districts in the neighbourhood of settlements. However, during historical times the process gathered momentum as settlements and populations expanded. For example, in Denmark, Iversen (1964, 1969) has shown that certain heathlands originated in Viking times (e.g. 740 and 830 A.D.), and there is evidence of considerable expansion of heathland both in England and Europe between 1100 and 1200 A.D. Land was required for cultivation and grazing, but the forests also suffered from demands for timber for both constructional purposes and for fuel. In particular, the use of charcoal for iron smelting resulted in forest destruction being carried into the more remote and upland areas. The resulting open country provided opportunities for increasing the scale of pastoral agriculture. With the advent of hardy breeds of cattle and, more especially, sheep, there was a progressive extension northwards in Europe of the use of the steadily expanding heathlands for grazing. Nowhere was this more apparent than in Britain, where the practice of grazing large flocks of sheep (mainly the Cheviot and Black-faced breeds) on heathlands, to the exclusion of all other domestic animals, extended from northern England into Scotland in the late eighteenth and nineteenth centuries.

Throughout Western Europe the heathlands proved useful for pasturing grazing animals, and

were especially valuable as a source of winter forage (Romell, 1951, 1952). For this reason, they were maintained and managed up to the latter part of the nineteenth century, but from that time onwards increasing intensification of agriculture in the more fertile districts reduced the value of heathlands. Throughout most of Western Europe and Scandinavia they have been progressively "reclaimed" for cultivation or afforestation. Only in northern England and Scotland are they still used extensively for sheep farming.

A further factor contributing to the survival of heathlands in Britain is the presence of the red grouse (*Lagopus lagopus scoticus*). Open heathland constitutes the natural habitat of this game bird, which increased considerably in numbers as a consequence of the expansion of heathlands. The interest of sportsmen in grouse shooting has more than compensated for some decline in the profitability of sheep farming. This has ensured, for the time being at least, the retention of large tracts of heathland in the upland districts of England and Scotland, which are managed as "grouse moors".

FIRE

The effects of regular management of European heathlands, particularly those in Britain, by fire are more fully discussed in Chapter 49. However, brief reference must be made here to fire as a factor of great importance in regard to both the origins and the continuance of many European heathlands. It is reasonable to suppose that, before human intervention was significant, localised fires due to natural causes were amongst the factors responsible for the occurrence of open patches in the forests of Western Europe, which on suitable soils were occupied by vegetation akin to that of heathland. After forest clearance, the value of open heathland for grazing purposes could only be sustained if trees were prevented from re-invading and *Calluna vulgaris* (the chief grazing plant) was kept in a productive condition. For reasons to be discussed in Ch. 26, Volume B, these objectives have generally been achieved by burning, and to a greater or lesser extent most West European heathlands (other than those at high altitudes or on the coast) have been subjected, from time to time, to fire (Fig. 14.10).

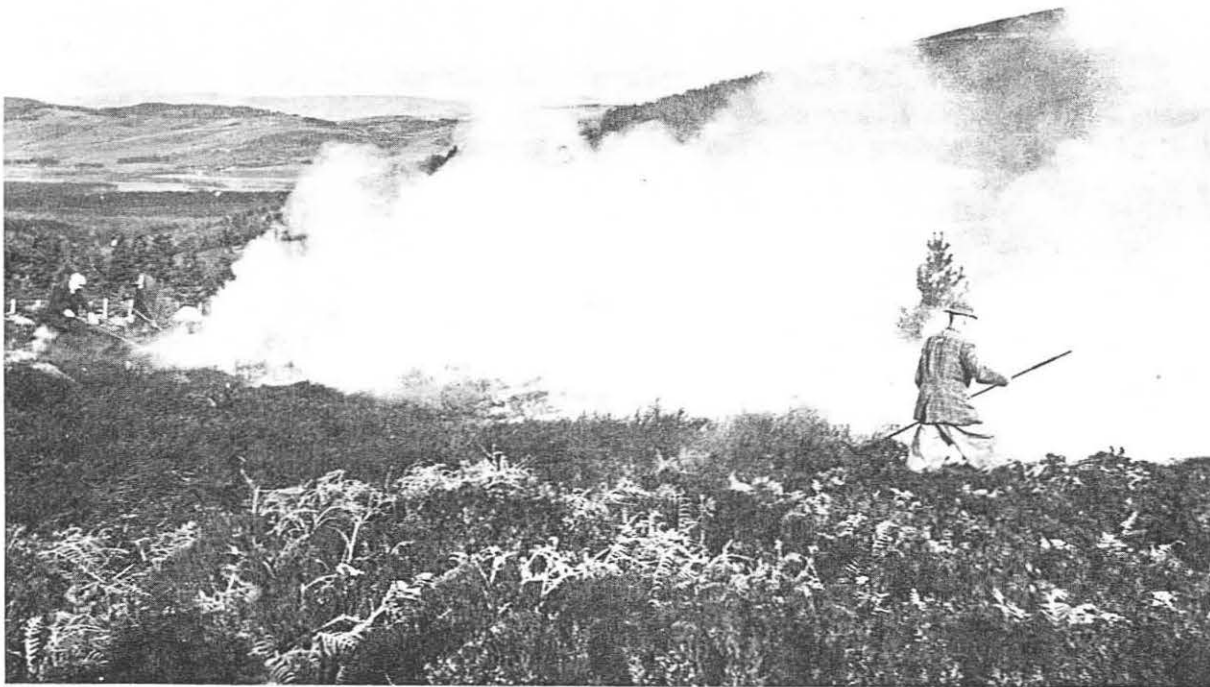


Fig. 14.10. Management of *Calluna*-heathland in Scotland by burning in March. (Dead fronds of *Pteridium aquilinum* in foreground.) (Photo C.H. Gimingham.)

Occasional burning probably has only a minor effect on the floristic composition of heathland communities. However, in so far as this factor contributes to the maintenance of heathlands, the vegetation may be said to be adapted to fire and to show some of the characteristics of a fire climax. The widespread dominance of *Calluna vulgaris* may, at least in part, result from the fact that it regenerates quite readily from stem bases which, especially when buried in litter or humus, may survive the passage of fire, and there is some evidence that seed germination is improved by short periods of heat pre-treatment (Whittaker and Gimingham, 1962).

When burning is relatively frequent, there is a considerable effect on floristic composition, which may be simplified and impoverished. This is particularly evident in Britain, where *Calluna vulgaris*, sometimes with an understorey of *Erica cinerea*,

may be virtually the only low shrub species. The remaining flora consists largely of relatively fire-resistant species such as *Potentilla erecta* (which has an underground tuberous rootstock), *Vaccinium myrtillus* or *Erica tetralix* (with rhizomes). Many typical heathland species are fire-sensitive (or sensitive to the combination of burning with grazing) and are consequently reduced or lacking: examples are *Juniperus communis*, *Genista anglica* and *Polypodium vulgare*. The diversity of bryophytes is also reduced, though a few remain as constant species of fire-managed heathland, e.g. *Pohlia nutans* (Shimwell, 1975). On the other hand, regular burning often encourages the development of lichen-rich heathland communities (Ward, 1970, 1971a, b), although again certain species are fire-sensitive.

Heathland communities in which vascular species other than *Calluna vulgaris* are very poorly

represented are therefore generally indicative of repeated burning. They have frequently been named *Callunetum vulgaris* (e.g. McVean and Ratcliffe, 1962), but it is usually possible to find fragments of stands which have escaped such severe treatment and are less impoverished. These generally indicate that the managed vegetation has been derived from one or other of the heathland community types to be described in the next section (Shimwell, 1975).

COMPOSITION — REGIONAL VARIATION

In general, European heathland communities are not floristically rich. None the less, their geographical area embraces an extensive range of climatic and edaphic régimes, resulting in considerable variation in community composition. This has been the subject of a large number of investigations, not least because the Zürich–Montpellier and Scandinavian phytosociological systems evolved in Europe with the result that, in common with other vegetation types, much discussion has centred on the problems of classifying heathland communities. While a substantial measure of success has been achieved in the search for an acceptable treatment of heathlands according to the Braun-Blanquet system, it is also evident that heathlands provide an excellent example of continuous variation in floristic composition and repay study on this basis. Both approaches have contributed conspicuously to an understanding of regional variation in the composition of heathlands (Gimingham, 1961, 1969, 1972).

An outline of the main trends of variation follows, using the primary division into dry-heathlands, wet-heathlands and mountain heathlands introduced on p. 367. In view of the fact that agreement is still lacking on the details of a phytosociological hierarchy, it is not possible to present any one system as generally accepted. However, correspondences will be indicated, as appropriate, to those categories which have received widest currency.

Dry-heathlands

Since 1949 these have very generally been included in a class named Nardo-Callunetea

(Preisling, 1949), though a number of authors have adhered to an earlier category, Calluno-Ulicetea, established by Braun-Blanquet and Tüxen in 1943. Each of these titles gives some indication of the major floristic affinities of the class. Within this, the bulk of European dry-heathlands are commonly assigned to the order Calluno-Ulicetalia (Tüxen, 1937), but certain communities in the extreme south of the heathland region are separated under Erico-Ulicetalia (Braun-Blanquet et al., 1964).

Throughout the dry and mesophilous heathlands of low and middle altitudes in Western Europe, *Calluna vulgaris* is an almost universal component, often dominant. However, this is inclined to give a false suggestion of floristic uniformity because, as indicated in a preliminary way by the division into the two orders referred to above, there are substantial differences between northern and southern heathlands, also between western (Atlantic) heathlands and those in more easterly situations (De Smidt, 1967). These trends follow climatic gradients, but superimposed on them are variations in composition related to the moisture and nutrient status of the soils and other factors such as management by burning. In addition, maritime influences are reflected in floristic composition, and dune heathlands, although related to the type characteristic of the geographical location, contain distinctive species [such as *Carex arenaria* and *Ammophila arenaria* (Fig. 14.11)].

Leaving aside for separate mention heathlands of the more highly oceanic, Atlantic seaboard of Europe, and starting in the north, a widely distributed type has been described as “boreal heather moor” (Birse, 1976), in which, in addition to *Calluna vulgaris*, species having northern patterns of distribution are strongly represented, notably *Vaccinium myrtillus*, *V. vitis-idaea* (Fig. 14.7), *V. uliginosum*, *Empetrum nigrum* and mosses such as *Hylocomium splendens* and *Pleurozium schreberi*. This type of community occurs in the Faerøerne islands, southern Norway, southern Sweden, Denmark, Scotland and northern England, becoming increasingly confined to north-facing slopes in districts further south, as for example in northern Germany and The Netherlands.

While *Calluna vulgaris* is very frequently the structural dominant, this is not always the case and one of the other ericaceous species may assume this



Fig. 14.11. *Empetrum nigrum* (right foreground) and *Calluna vulgaris* on stabilised sand-dune, accompanied by *Ammophila arenaria*, *Festuca rubra* and lichens. (Photo C.H. Gimingham.)

rôle. Their contribution to the community varies considerably: for example *Vaccinium myrtillus* is particularly associated with the more northerly and oceanic heathlands from Norway to northern Germany, becoming dominant even to the exclusion of *Calluna vulgaris* on exposed, windswept ridges in northern England. These communities may contain a number of species with strongly oceanic affinities, for example *Blechnum spicant* and, particularly in southwestern Norway and Britain, *Erica cinerea*.

Vaccinium vitis-idaea contributes to many of these heathlands in southern Norway, Sweden (Malmer, 1965) and Scotland (Gimingham, 1964), and is especially characteristic of the inland heathlands of Jutland (Denmark), where the more strongly oceanic species tend to be reduced. Very similar heathland-types occur in upland districts of Belgium (see p. 386). Throughout the areas mentioned, *Empetrum nigrum* is a frequent component, sometimes dominant. It appears to be best represented in the heathlands of rather more oceanic regions than those of which *Vaccinium vitis-idaea* is characteristic, notably along the western fringes of southern Sweden, Jutland (Denmark), and The Netherlands. In these regions it also contributes strongly to coastal dune heaths,

and corresponding communities occur on the coasts of Scotland.

A further species of importance in some examples of boreal heathland is *Arctostaphylos uva-ursi*, which is described by Bøcher (1943) as a "boreal dry soil plant" and tends to occupy soils of rather higher nutrient status, with less raw humus accumulation, than those of the communities already mentioned. It occurs under strongly oceanic conditions in southwestern Norway and is a constant of a well-defined community from the eastern central uplands of Scotland (investigated by Ward, 1970, 1971a, b), but it is also well represented in certain heathlands of southwestern Sweden (province of Halland) and Denmark where subcontinental conditions are approached.

Bøcher (1943) divided these communities into two alliances — Myrtillion boreale and Empetrium boreale. Owing however to the complex variation in composition, they have commonly been united in one alliance, sometimes termed Myrtillion (Bridgewater, 1970) but perhaps more commonly Empetrium boreale, as in Birse (1976), or Empetrium nigri (Schubert, 1960).

In the region of southern Scandinavia (Damman, 1957), northern Germany, and The Netherlands there is overlap, or intergradation,

between this boreal heathland type and a group of communities generally united in the alliance Calluno-Genistion (Duvigneaud, 1944). In the latter, species of northerly distribution are reduced in quantity, or lacking, and others with more southerly affinities are prominent. Among these are *Genista anglica* (a plant which also belongs to some of the boreal heathlands, for example in Scandinavia and Scotland, where it is specially abundant in the *Arctostaphylos uva-ursi* communities), particularly in the more oceanic districts, *Genista pilosa* in suboceanic areas, and *G. germanica* and *G. tinctoria* in subcontinental parts. Another widespread characteristic species is *Cuscuta epithymum*. In general the bryophyte flora of these heathlands is poorer than that of boreal heathlands, whereas the lichen component may be diverse. Northern outliers of this heathland type occur in southern Sweden, Denmark and southeastern England, but it becomes increasingly extensive in northern Germany, The Netherlands and Belgium, and intergrades with other types in northern France.

All these communities may include varying amounts of a tall shrub component, notably *Juniperus communis* (Fig. 14.3). This species, however, is poorly represented in most British heathlands (perhaps due to the long history of grazing and burning), and tends to become less prominent southwards from The Netherlands. *Ulex europaeus* is also widely present in heathlands, and (especially in parts of northern France and Britain) may be very abundant, with a tendency to become dominant to the extent of completely excluding heathland vegetation. Its status in heathland vegetation is, however, uncertain, and has probably been enhanced by soil disturbance. *Sarothamnus scoparius* is a further tall shrub species which contributes quite widely to heath communities, particularly those in a sector extending from the south of The Netherlands to northern France, and has been used in naming an alliance Sarothamnion scopariae (Preising, 1949, quoting Tüxen, unpublished).

Heathland communities of the more highly oceanic western margins of the region have certain distinctive features. While they have generally been included in the same order as those surveyed above, a recent treatment (Géhu, 1975) separates them under Ulicetalia minoris, with the com-

munities belonging mainly to the north, northwest and more easterly areas (described above) constituting the order Vaccinio-Genistetalia. In the most westerly parts of southern Norway *Erica cinerea* is very strongly represented in the heathland communities. Although they share a number of plants with heathlands of the northerly Empetrium boreale, the presence of a group of species having markedly western distribution patterns, such as *Carex binervis*, is distinctive. Closely similar communities occur in northern and northwestern Scotland (Fig. 14.12) and in Ireland. Continuing southwards, *Erica cinerea* remains characteristic of strongly oceanic heathland types, especially in northern France, but also in southwestern France and northern Spain. However, from Ireland and Wales southwards, low-growing species of *Ulex* become an integral part of these communities (Fig. 14.13). In the most oceanic parts (Ireland, Wales, southwestern England, northern and northwestern France) *Ulex gallii* is important. *Ulex minor* replaces *U. gallii* eastwards from the county of Dorset in southern England, and is also very prominent in the oceanic heathlands of northern France, extending west and south where it is often mixed with *U. gallii*. All these oceanic heathlands are commonly linked in the one alliance Ulicion minoris (=Ulicion nanae; Duvigneaud, 1944), but some authors recognise a separate alliance, Ulicion gallii (Des Abbayes and Corillon, 1949).

An additional ericaceous species which has an outlying station in the extreme southwest of Britain, *Erica vagans*, becomes significant in many of the oceanic heathland communities of northern France and extends southwards into Spain. In the southwest of France and in the Basque and Cantabrian regions of Spain (Dupont, 1975) this species, together with *Daboecia cantabrica* (which also has outlying stations in the British Isles, in western Ireland), forms part of a community of great floristic richness which has been variously linked with the Ulicion minoris or with an alliance named Ericion umbellatae (Braun-Blanquet et al., 1952) (=Cistion hirsutae; Braun-Blanquet et al., 1964). This lack of uniformity in practice emphasises the difficulties in achieving a satisfactory hierarchy of categories, especially in view of the fact that the latter alliance is commonly placed in a different order, the Erico-Ulicetalia, from that to



Fig. 4.12. Oceanic, maritime heathland-type containing *Calluna vulgaris*, *Erica cinerea* (in flower) and low-growing *Juniperus communis*. North coast of Scotland (Photo C.H. Gimingham.)



Fig. 14.13. *Calluna vulgaris*–*Ulex minor* heathland, Dorset, south England. (Photo C.H. Gimingham.)

which the former is assigned. The order Erico-Ulicetalia comprises southerly heathland and scrub types which contain a variety of ericaceous species with predominantly southern, often Mediterranean patterns of distribution, such as *Erica umbellata*, *E. mackaiana*, *E. australis* ssp. *aragonensis*, *E. arborea*, *E. mediterranea*. These communities occur mainly in southwestern France, and in the coastal lowlands of northern and northwestern Spain, extending into Portugal. In the latter areas, the heath species are increasingly associated with taller, larger leaved shrubs, for example species of *Cistus*. When these predominate in the vegetation, the term scrub (e.g. maquis-scrub) applies instead of heathland.

Many of the heathland communities referred to in this section show variations in composition related to the nutrient status of the soil. This bears in particular on the prominence of grass species which, in addition to a variety of forbs, increase in importance as nutrient status increases. Communities in which this trend is most evident are often described as "herb-rich" or "species-rich", and plants such as *Viola riviniana*, *Thymus drucei*, *Lathyrus montanus*, *Hypericum pulchrum*, *Lotus corniculatus* and *Campanula rotundifolia* may be cited as indicators.

Wet-heathlands

In all parts of the heathland region there are gradients from dry, freely drained soils through moist soils with varying degrees of impedence of drainage, to those which are waterlogged for varying periods of the year, leading often to peat formation. The corresponding gradients in floristic composition have been divided into categories such as "dry", "mesophilous", "humid" and "wet". Most of the dry-heathland community types mentioned in the foregoing section have "mesophilous" (or "moist"), and "humid" variants. For example, within the Ulicion *nanae* in northern France and southern England there is a distinctive "mesophilous" community (Géhu, 1975) containing *Erica ciliaris* along with *Calluna vulgaris* and *Erica tetralix*. In similar habitats in western France, *Erica scoparia* may be associated with this group of species. Where the description "humid" has been applied, *Erica tetralix* is abundant, in association with species derived from the "dry" end

of the gradient such as *Calluna vulgaris*, *Ulex minor* or *U. gallii* etc., and others from the "wet" end such as *Molinia caerulea*.

Communities which are properly described as wet-heathland, however, are commonly separated into a completely different class, Oxycocco-Sphagnetea. As the title indicates, the class is distinguished by the important role of *Sphagnum* spp. Within it various names have been given to groups of wet-heathland communities, generally stressing the significance of *Erica tetralix* [e.g. order Ericetalia tetralicis (Moore, 1968); alliance Ericion tetralicis (Schwickerath, 1933)]. In addition to the plants already mentioned, there are varying contributions from graminoid species such as *Molinia caerulea*, *Eriophorum vaginatum*, *Juncus squarrosus* and *Trichophorum caespitosum*, while *Polytrichum commune* is often present, forming large clumps. Geographical variation in composition is, in general, rather less in wet- than in dry-heathlands. However, in the northern part of the region *Empetrum nigrum* is a conspicuous component of some wet-heathlands, while *Erica ciliaris* and *E. scoparia* distinguish southern wet-heathlands.

Mountain heathlands

Heathlands at the higher altitudes are distinctive in structure (see pp. 367, 369), and also to a considerable extent in composition. There may be an arctic-alpine element in the flora, in addition to a number of species such as *Vaccinium myrtillus*, *V. vitis-idaea*, and *V. uliginosum*, which as well as being typical of the more northerly lowland heathlands are tolerant of subalpine and low-alpine conditions. These occur widely in heathlands on European mountains.

It is possible here to give only a very general indication of the extensive range of dwarf heathland communities. The transition between sub-alpine scrub (fringing the upper limit of forest) and low-alpine dwarf-shrub heathland is often the habitat of a dwarf juniper (*Juniperus communis* ssp. *nana*) community, with *Calluna vulgaris* and other ericaceous species such as *Arctostaphylos uva-ursi* or *Arctous alpinus*. Communities of this type occur from Scandinavia and Britain to the mountains of southern Europe, and have been grouped in an alliance Juniperion *nanae* (Braun-Blanquet et al.,

1939). Dwarf *Calluna vulgaris* is widely dominant in heathlands above the natural timberline, although it disappears at the higher altitudes. A community in which *Calluna vulgaris* and the moss *Racomitrium lanuginosum* together form a low, dense carpet is found on mountains under the oceanic conditions of northern Britain (giving place to *Racomitrium-Empetrum* heathland at higher altitudes), while dwarf *Calluna-Vaccinium* (*V. vitis-idaea* and *V. myrtillus*) heathlands are more widespread, in both oceanic and suboceanic areas, for example in Scandinavia (Nordhagen, 1928, 1936), Britain, Germany (Harz, Sauerland), Belgium and France (including *Calluna-Vaccinium myrtillus* communities in the Pyrenees). Avoiding the more oceanic regions are heathlands with *Phyllodoce coerulea* (suboceanic-subcontinental, Bøcher, 1943), and *Cassiope tetragona* (subcontinental-continental). On soils of relatively high nutrient status herb-rich subalpine heathlands occur, for example the *Calluna-Antennaria dioica* association.

A further factor which profoundly affects the composition of mountain heathlands is the duration of snow cover (Dahl, 1956). This is particularly evident on examination of the range of communities lying above the limits of *Calluna vulgaris* as a dominant. In exposed areas where snow cover is thin and of relatively short duration, *Loiseleuria procumbens* is often the chief species, giving its name to an alliance, *Loiseleurieto-Vaccinium*, which is represented in almost all the major mountain systems of Europe. In similar situations on calcareous soils *Dryas octopetala* (Rosaceae) heathlands are found, in which this species is often mixed with *Empetrum hermaphroditum*. The latter, along with *Vaccinium myrtillus* and *V. uliginosum* forms communities, frequently rich in lichens, where snow cover lasts longer. A very similar community, generally rich in bryophytes, is associated with snow beds. In the Alps and other mountains of southern Europe the series is completed by a taller and particularly handsome community containing *Rhododendron* species (notably *R. ferrugineum*) where the protective snow cover lasts longest. The *Vaccinium* and *Rhododendron* heathlands are commonly grouped in *Rhodoreto-Vaccinium*, belonging, with the *Loiseleurieto-Vaccinium*, to the order *Vaccinio-Piceetalia* (class *Vaccinio-Piceetea*). This arrange-

ment expresses the floristic relationships between montane forest vegetation and the dwarf heathlands above its limits.

SUCCESSION

Only those heathlands which belong to altitudes above the timberline, and perhaps certain types of wet-heathland on peat and exposed maritime heathlands, can be regarded as stable or semi-stable. Most of the rest of the European heathlands are either seral or are perpetuated as heathlands by continued management.

Successions involving heathland communities are of two main types. The first comprises vegetation and habitat changes in peat bogs. These may result from long-term shifts of climate, leading to progressive reduction in the ombrogenous supply of water to bog surfaces. Analysis of peat deposits indicates successional trends involving increases in the quantities of *Erica tetralix* and *Calluna vulgaris*, with the establishment of wet-heathland in place of bog. Continuance of this trend has led, particularly in more continental regions, to replacement of heathland by scrub or woodland on the drained and aerated peat, but reversal of the climatic trend (such as occurred at the Subboreal-Subatlantic transition) brought about in the more oceanic areas a return of the bog vegetation, usually with dominance of *Sphagnum* species.

The second main type of succession which includes heathland is that on non-calcareous coastal sand dunes. In many parts of the Atlantic coasts of Europe, heathland develops on stabilised dunes, when sand accretion has largely stopped and the pH has fallen to about 6.5 or less. At this stage, *Calluna vulgaris* and in some areas *Erica cinerea* (western Britain, northern France) or *Empetrum nigrum* (Scotland, western Scandinavia, The Netherlands), can colonise the patches of bare sand which remain among the shoots of species such as *Ammophila arenaria*, *Carex arenaria* and *Festuca rubra* (Fig. 14.11). In view of the rarity of seedlings of the heathland plants, it seems probable that suitable conditions for forward colonisation by heathland species in a developing dune system occur infrequently, and that the succession proceeds intermittently rather than continuously. It may also be considerably affected by rabbit-

grazing in some areas (Gimingham, 1972). In time, where seed-parents of shrubs and trees are present, the succession may proceed to scrub and woodland, but this is often prevented by human interference.

In the same way, most lowland heathlands are potentially dynamic and, if management ceases, may be invaded by tall shrubs or trees (Fig. 14.9). The most rapid invaders are often *Betula* spp. (*B. pubescens*, *B. pendula*), *Juniperus communis* and *Sorbus aucuparia*. In appropriate parts of the heathland region other shrubs which colonise heathlands include *Sarothamnus scoparius*, *Frangula alnus*, *Prunus spinosa* and *Crataegus monogyna*, and tree invaders may be *Quercus* spp. (*Q. robur*, *Q. petraea*) or *Fagus sylvatica*. However, the time required for the entry of tall shrub or tree species depends not only on the rate of arrival of their seeds, but also on the structure of the heathland community concerned. In the case of *Calluna vulgaris* communities, this varies considerably in relation to the age structure of the stand and the growth phase of individual plants of *Calluna vulgaris*.

CALLUNA VULGARIS

Because *Calluna vulgaris* is for various reasons so often the dominant species in European heathlands (Gimingham, 1960), a regional survey is incomplete without special mention of its influence on the structure and dynamics of these communities. In all but the mountain and wet-heathlands, the life span of an individual plant normally lasts between 30 and 40 years. During this time the processes of growth and maturation lead to various changes in the general morphology of the plant (Fig. 14.14), which were first described by Watt (1955) under the following headings:

The pioneer phase. In the early stages of development the shape of the young plant is more or less pyramidal, with rather regular branching from the axis of a single 'leader'. However, the apex of the leading shoot seldom continues growth for more than two seasons, when it is replaced by two or more branches arising just below the tip (Fig. 14.7), while other laterals become equivalent to the leader, producing a radiating, bushy type of

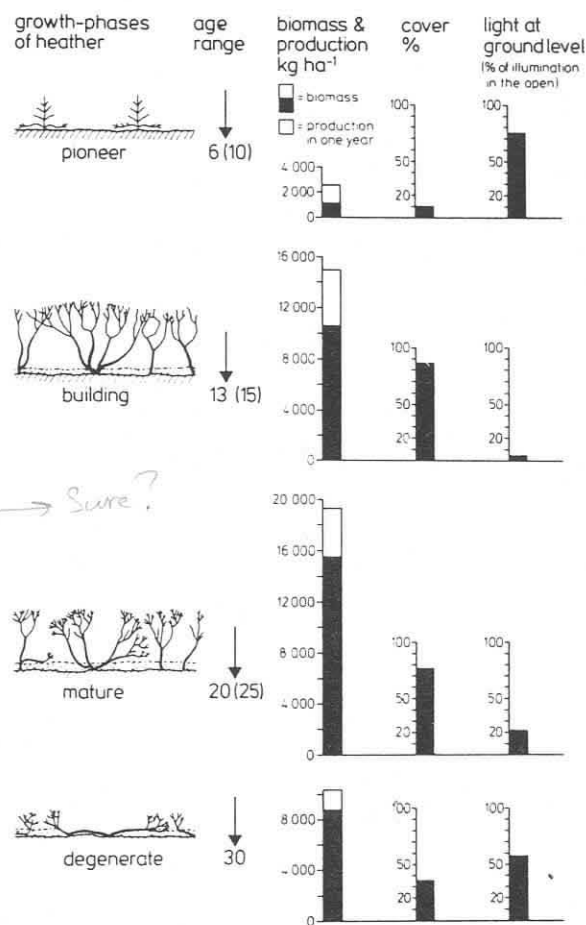


Fig. 14.14. Diagram illustrating the four growth-phases of *Calluna vulgaris*, and associated changes in biomass and production, cover and illumination at ground level.

growth. In normal habitats, the plant has lost the appearance of a pioneer before it is 6 years old. By this time, the scattered or clustered pioneer plants have expanded, and cover has increased, often approaching 100%.

The building phase follows, normally until the plant is rather over 15 years old. Productivity of peripheral green shoots is high, as is the ratio between the weight of these and that of the woody framebranches, though this decreases with age. Flowering is profuse. Isolated plants are hemispherical in shape, but in a dense stand a canopy forms at about 30 to 40 cm above the ground, borne on branched woody stems. In either case very little light penetrates to ground level and

vigorous heath in this phase excludes most other species.

The mature phase, lasting often until the plant is well over 20 years old, is characterised by some reduction in extension growth at the periphery, where the leaf-bearing shoots become more condensed and usually darker in colour. The middle branches begin to separate, in time forming a central gap which allows increased illumination at ground level, and air circulation within the bush.

The degenerate phase is marked by further collapse of the central branches (often under the weight of winter snow) and their death, progressively from the middle of the bush outwards, extending the gap (Fig. 14.15). For a time, the peripheral branches may remain alive, because frequently they have become partially buried in moss, litter or humus and have produced adventitious roots. Dead branches remain visible in the centre of the patch,

surrounded by a ring of living shoots which may, temporarily, remain quite dense. Eventually the whole dies back.

In a *Calluna*-dominated heathland, where the population of this species is uneven-aged, plants of each of these growth phases exist side by side producing an uneven, patchy structure (Watt, 1947). The effects of *Calluna vulgaris* on the micro-habitat change very substantially as it passes through the sequence of growth phases, altering the possibilities for other species to co-exist with the dominant in a given patch (Barclay-Estrup, 1970, 1971). As a result, on any one patch, as *Calluna vulgaris* passes through its sequence of phases there are accompanying changes in the diversity and cover contribution of other species (Fig. 14.16).

The number of associated species and their cover usually reach their maximum while *Calluna vulgaris* is in the pioneer phase, for often there are patches of bare ground available for colonization,



Fig. 14.15. Degenerate bush of *Calluna vulgaris*. The central branches are all dead, creating a gap which is colonised by bryophytes and lichens (*Parmelia physodes* on old branches of *Calluna*). (Photo C.H. Gimingham.)

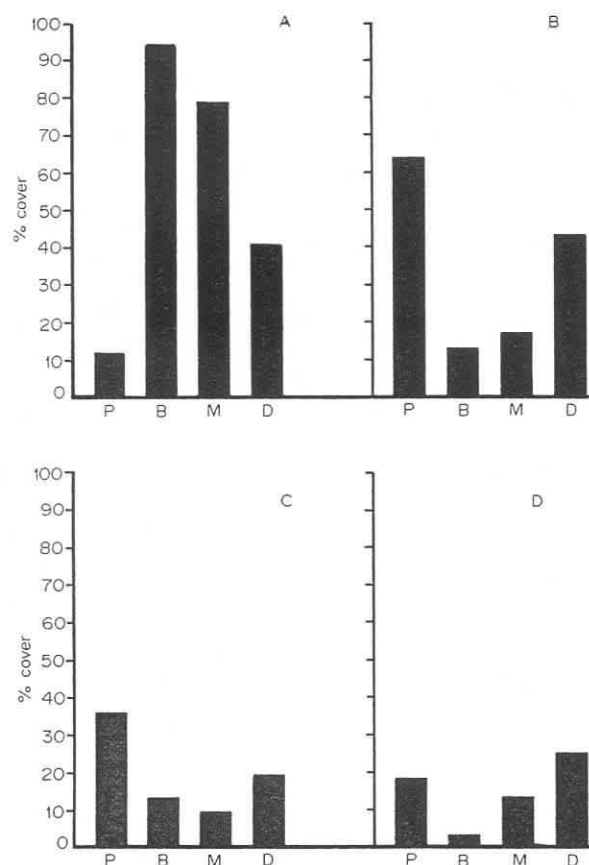


Fig. 14.16. Histograms showing the cover contribution of various categories of the vegetation in areas occupied by *Calluna vulgaris* in each of its growth-phases (data from nine 1-m² quadrats). From Barclay-Estrup and Gimingham (1969). A. *Calluna vulgaris*. B. Other dwarf-shrubs. C. Graminoid herbs. D. Bare ground and lichens.

Legend: P=pioneer phase; B=building phase; C=mature phase; D=degenerate phase.

while spreading plants may grow into the spaces between the young individuals of *Calluna* (Table 14.5). As the latter coalesce and enter the building phase, they begin to exert their greatest effect and the contribution of other species declines, almost to the point of extinction. When, however, the canopy begins to thin out in the centre of the bush with the onset of the mature phase, the first plants to recolonise the ground below are shade-tolerant bryophytes such as *Hypnum cupressiforme* ssp. *ericetorum*. Later, as the gap develops, the patch of this moss may be invaded by others, such as *Pleurozium schreberi* and *Hylocomium splendens*. When the degenerate phase is reached, not only is

TABLE 14.5

Number of species of vascular plants per 4 m² in *Calluna vulgaris* stands of various ages: Perthshire, Central Scotland

Phase	Age of <i>Calluna</i> stand since last fire (years)	Number of species of vascular plants
Pioneer	3	15
Late pioneer	5–6	22
Building	8	16
Late building	13–14	11
Late mature	c. 25	14

there normally a period in which both bryophytes and lichens increase in abundance and cover, but also various vascular plants spread in or colonise, such as *Arctostaphylos uva-ursi*, *Vaccinium* spp., *Empetrum nigrum*, *Deschampsia flexuosa* and *Dryopteris dilatata*.

Evidence has been presented (Watt, 1947; Barclay-Estrup and Gimingham, 1969) for regarding this process as, in many instances, cyclical (Fig. 14.17). On occasion, if bare ground is exposed in the centre of a degenerate bush, young plants of *Calluna* may be able to establish before or along with other species, fairly rapidly re-occupying the space. More frequently, however, the developing community of other species prevents this but after they have progressed through their own developmental sequences their cover declines and this is the opportunity for *Calluna* to re-invade and commence the cycle anew. Allowing for up to 30 years of occupancy of a site by an individual of *Calluna*, and perhaps nearly as much again by other species, the whole cycle may sometimes require over 50 years for completion. Such cycles are therefore only in evidence in heathlands where management by burning or grazing is absent or minimal, but under these conditions the number of species participating in a heathland community, in association with dominant *Calluna vulgaris*, may be quite large.

It is especially in the gap phase (i.e. the period extending from the onset of degeneracy in an old bush to the arrival of new pioneer plants in the gap), that associated species have their chief opportunity. By the same token, it is in this part of the cycle that there is opportunity for foliage of a competitor such as *Pteridium aquilinum* to appear (Watt, 1955), or for the establishment of seedlings of shrubs or trees. When this occurs further

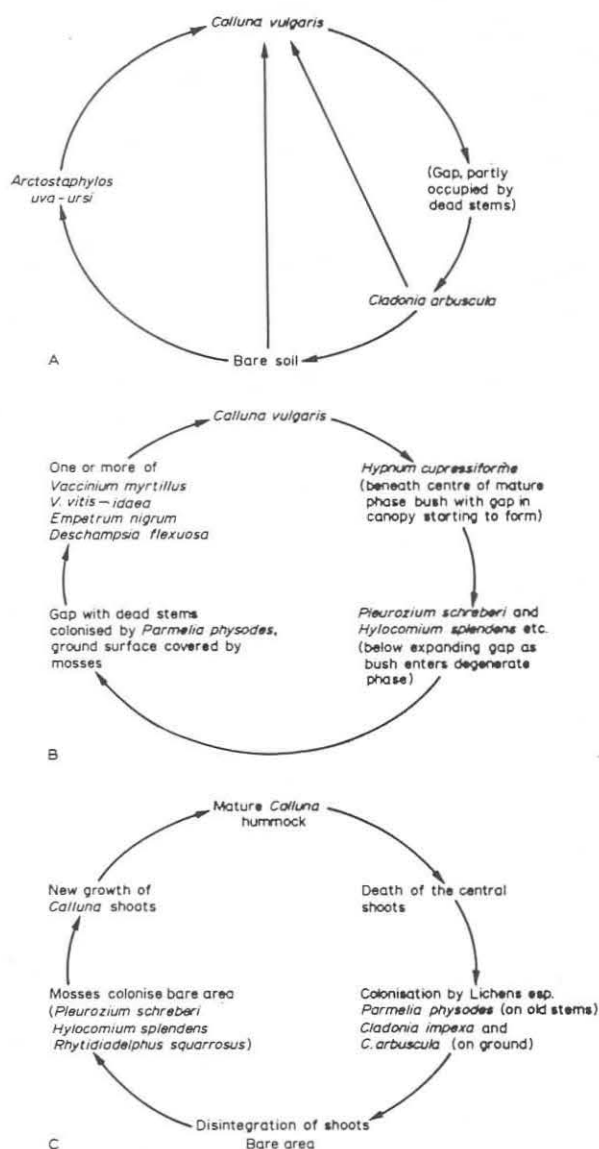


Fig. 14.17. Examples of cyclical change in *Calluna*-dominated heathland communities. A. In a *Calluna vulgaris*–*Arctostaphylos uva-ursi* community, east central Scotland (after Watt, 1947). B. In a *Calluna vulgaris*–*Vaccinium* community. C. In a dune heathland.

changes are likely to be successional in nature rather than cyclical.

Managed stands, unlike those just discussed, are even-aged, because regeneration following a fire is normally uniform and synchronous. Where vegetative regeneration predominates the pioneer phase is abbreviated and the stand may pass in a very few years into the building phase. It is the objective of

burning to maintain as much as possible of a heathland area in the building phase, and to prevent any stand progressing into the mature or degenerate condition. Hence, much of the area is occupied by what is virtually a monoculture of *Calluna vulgaris* in its most vigorous and exclusive condition. It is, therefore, not necessarily the direct effects of fire which alone explain the floristic impoverishment of managed heathlands (p. 380), but also the indirect (competitive) effects of *Calluna* monocultures in the building phase.

A similar comment may be applied to the prevention of invasion by shrubs and trees in heathlands. Fire, in itself, often creates ideal conditions for the germination of their seeds and establishment of seedlings (e.g. *Betula* spp., Table 14.6; *Pinus sylvestris*). However, if re-establishment of a *Calluna* canopy is rapid and thorough, there is high mortality of tree seedlings (Table 14.6). When this effect is reinforced by grazing, elimination may be complete; but otherwise some may survive (especially when a good seed year has produced seedlings in large numbers on a burnt patch).

TABLE 14.6

Numbers of individuals (seedlings and young trees) of birch (*Betula pendula*) in areas of 20 m² in *Calluna vulgaris* stands of various age: Dinnet Muir, Aberdeenshire, northeast Scotland (the stands in each site were close together, on level ground and similar soil; they were within 15 m of mature birch trees producing abundant seed)

<i>Calluna vulgaris</i> stands		Numbers of <i>Betula pendula</i> (means of two replicates ± standard error)
phase	age (years)	
Site 1		
(Recently burnt)	1-2	55.0 ± 21.0
Late pioneer	8+	6.5 ± 0.5
Building	10-12	3.0 ± 0
Early mature	15	0.5 ± 0.5
Degenerate	> 18	1.0 ± 1.0
Site 2		
(Recently burnt)	1-9	268.0 ± 162.0
Late pioneer	7-9	6.5 ± 0.5
Building	11-13	2.5 ± 0.5
Early mature	14	1.0 ± 0
Degenerate	> 20	0.5 ± 0.5

Data from Dr. W.K. Gong.

PRODUCTION AND ORGANIC MATTER ACCUMULATION

When used in its strictest sense the term heathland applies to areas where some member of the Ericaceae dominates the vegetation. In a wider sense however, the term is often used to describe a particular kind of countryside or scenery that includes a number of associated types of vegetation such as bracken (*Pteridium aquilinum*), gorse (*Ulex* spp.), birch scrub (*Betula* spp.) and a range of peatland and mire communities. Although it would be interesting to discuss patterns of primary production and accumulation of organic matter in relation to succession, soil, climate and land use for such a range of vegetation types, the most that can be attempted for European heathlands at the present is to make comparisons between areas dominated by the common heather (*Calluna vulgaris*). The following account will concentrate upon areas of mineral soils rather than soils which are primarily organic in content.

Estimates of primary production may have been undertaken by different workers for a number of reasons, and to a great extent these reasons determine the data that are available for discussion and comparison. Production data may have been obtained for comparisons of apparent efficiency or function between types of vegetation, or between similar types occurring at different sites. Reliable estimates of standing crop and primary production are an essential prerequisite for the construction of nutrient budgets and analysis of energy flow, both of which are important in attempting to understand the functional relationships within any biological community. In a system such as heathland where nutrients are in short supply the measurement of inputs, losses and storage are especially important, and an understanding of such factors is of value when considering the possible effects of management processes that may well have long-term consequences for the overall dynamics and survival of the system.

There is an obvious set of relationships between production, decomposition, grazing and the resultant accumulation of organic matter and nutrients in the ecosystem. Such relationships between litter production, loss and accumulation in forests (Jenny et al., 1949; Nye, 1961; Olson, 1963) and blanket bog (Gore and Olson, 1967) have been

examined using mathematical models that assume the attainment or existence of steady-state conditions. Where such conditions can be assumed it simplifies matters, but in the case of heathland ecosystems it soon becomes apparent that the majority of sites are by no means in such a state. The application of Watt's development phases (Watt, 1947) to heathland studies (Barclay-Estrup, 1970; Chapman et al., 1975a, b; Chapman and Webb, 1978; see also pp. 387–390) demonstrates this point. Production and associated processes within the heathland ecosystem are clearly related to this developmental sequence and any results obtained must therefore be considered and discussed against the age of the vegetation. As the standard definitions of the heathland development phases (see Gimingham, 1972, pp. 125–127) are subjective, and levels of production are not constant throughout any single phase, it would be more satisfactory to sample a series of sites of different ages and make use of growth or accumulation curves (Chapman et al., 1975a, b). This approach however can only be used where a sufficiently complete age series exists, and many prevailing management practices and accidental fires make older stands of heather rare or non-existent in many areas.

The mode of growth and pattern of shoot development in *Calluna vulgaris*, as described by Mohamed and Gimingham (1970), has been important in determining the methods used and the particular parameters measured by workers investigating the primary production of heath and moorland areas. The current year's growth of shoot material is in the form of new lateral green material, leading long shoots that may bear flowers, and recognisable growth increments to previous years' short shoots. Short shoots may persist for up to four years, depending upon the locality and the particular site. This mode of growth and pattern of shoot survival results in a litter-producing system that is dependent upon up to four years of green shoot production. The flow and interrelationships of organic matter through *Calluna* in the heathland system are shown in Fig. 14.18, where the compartments on the upper line represent the components of net primary production.

Whilst estimates of primary production and organic matter accumulation have been made on a number of European heathlands, only relatively

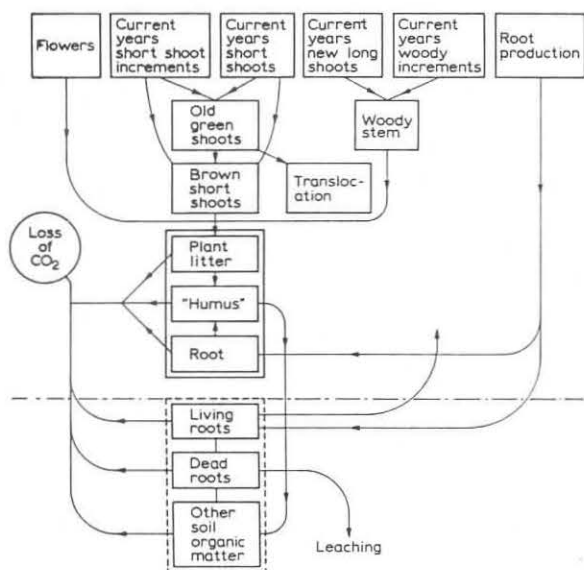


Fig. 14.18. Box model representing the transfer of organic matter in the growth of *Calluna vulgaris*. (From Chapman and Webb, 1978.)

little published work allows direct comparisons to be made at the level of total above-ground net production. In a number of cases the work was carried out with the principal object of assessing production of potentially edible material for animals such as sheep or grouse (*Lagopus lagopus scoticus*).

Above-ground standing crop

The relationship between the age of the vegetation and the weight of the above-ground standing crop for one particular area is shown in Fig. 14.19 where an age sequence obtained from lowland heathland in southern England has been fitted with a Gompertz growth curve (Fig. 14.19) from an age of three years onwards. Chapman et al. (1975a) have shown that the deviation from such a fitted curve during the first three years is due to the pattern of green shoot production and survival. It can be seen from the data shown in Fig. 14.19 that, if rates of increment of standing crop are to be obtained from consecutive estimates of the standing crop, then variable and even negative results may well be obtained, unless considerable effort is taken in selection of size and numbers of samples. To some extent this problem is reduced where an age series can be sampled and an averaged estimate

of the rate of increase in the standing crop obtained. This latter approach however is often restricted by the availability of older aged stands of heather, demonstrated in Fig. 14.20 where the majority of determinations of above-ground standing crop from a range of heathlands in Europe are from sites less than twenty years old. It is difficult to make many comparisons from data such as those shown in Fig. 14.20, especially when confidence limits of the individual means are taken into account. When only younger stands of heathland are considered (up to c. 15 years) an impression is gained of surprising uniformity in rates of increase of standing crop. Differences between the fast and slow rates of recovery following different intensities of burning at Kerloch Moor (Miller and Watson, 1974b) are almost as great as those shown by the data from all the other sites included in Fig. 14.20.

When trying to compare heathland sites on the basis of standing crop, or indeed any other

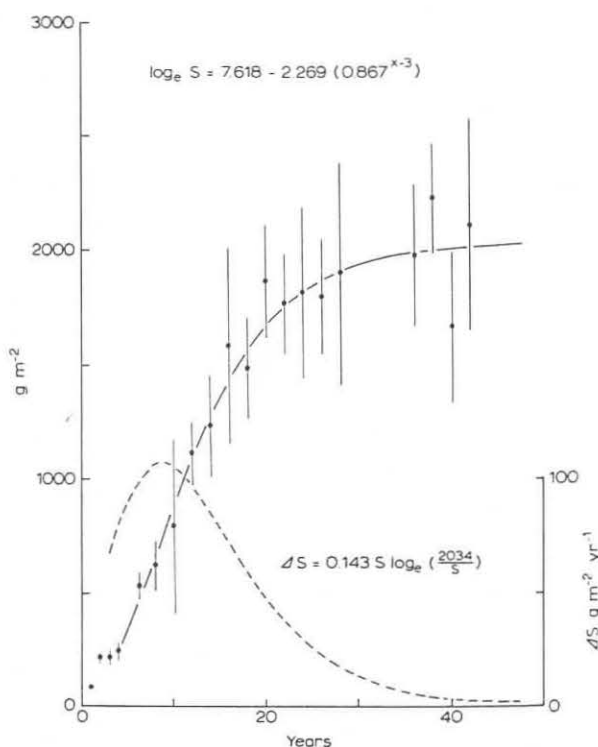


Fig. 14.19. Standing crop (continuous line) and rate of increment (pecked line) of the above-ground components of *Calluna* from Dorset heathlands in relation to their age with 95% confidence limits (from Chapman et al., 1975a).

TABLE 14.7

Data sources and symbols used for derivation of graphs

<i>Scotland</i>		
★	Glen Muick, Aberdeen	Moss (1969)
●	Lochnagar, Aberdeen	Moss (1969)
⊗	Corndavon, Aberdeen	Moss (1969)
▼	Kerloch Moor, Kincardineshire	Moss (1969), Miller and Watson (1978), G.R. Miller (pers. comm.) Grant (1971)
▽	Glensaugh, Kincardineshire	
☆	Elsick, Kincardineshire	Barclay-Estrup (1970)
△	Cairngorms	Summers (1972)
◇	North Cairn o'Mount Kincardineshire	Robertson and Davies (1965)
◆	Polworth Moss, Berwickshire	Robertson and Davies (1965)
▲	Listonshiels, Midlothian	Robertson and Davies (1965)
<i>Northern England</i>		
■	Blanchland Moor, Northumberland	Robertson and Davies (1965)
□	Teesdale, Durham	Bellamy and Holland (1966)
☆	Moor House, Westmorland	Forrest (1971), Forrest and Smith (1975)
<i>Eastern England</i>		
★	Cavenham Heath, West Suffolk	Chapman (unpubl.)
☆	Lakenheath Warren, West Suffolk	Chapman (unpubl.)
☆	Westleton Heath, East Suffolk	Chapman (unpubl.)
<i>Southern England</i>		
●	Dorset Heathlands	Chapman (1967), Chapman et al. (1975a, b)
○	New Forest, Hampshire	Chapman (unpubl.)
★	Woodbury Common, Devon	Chapman (unpubl.)
✱	Dartmoor, Devon	Chapman (1967, unpubl.)
✱	Exmoor, Somerset	Chapman (unpubl.)
☆	Penhallow Moor, Cornwall	Chapman (unpubl.)
★	Chapel Porth, Cornwall	Chapman (unpubl.)
<i>Sweden</i>		
☆	Skånör	Tyler et al. (1973)

parameter of performance or production, it is difficult to separate the effects of climate from those of soil. In the British Isles, heathlands in the south are mostly lowland and upon infertile soils where the larger part of the nutrient capital is contained within the organic matter of the litter and root zone (Chapman, 1970). Heathlands in the upland areas of Britain occur mostly in Scotland and the north of England, where climatic conditions are generally less favourable for plant growth but the soils are often more fertile. The apparent similarity of the heathland growth curves from different areas may therefore partly be the result of interaction of climate and soil nutrient factors. The information shown in Fig. 14.20 includes results from two different granite areas, from Dartmoor in the southwest of England (altitude *c.* 420 m), and from Kerloch Moor in eastern Scotland (altitude *c.* 150 m). The mean summer temperatures on Dartmoor are in the order of 2°C higher than at Kerloch Moor and the standing crops at comparable ages from Dartmoor are also consistently higher (Fig. 14.21).

Litter production

Estimates of litter production by heathland vegetation have been published by only a few authors and are shown in Fig. 14.23. Litter production has been measured by the use of litter traps (Cormack and Gimingham, 1964; Chapman, 1967; Forrest, 1971; Tyler et al., 1973; Chapman et al., 1975a; Forrest and Smith, 1975) and estimates of potential litter production (Fig. 14.22) based upon shoot and flower production have been described by Chapman et al. (1975a). In this latter work it was thought that such estimates of potential litter production were more reliable than trapping results from younger and more open heathland, where loss due to wind blow was shown to be significant.

Calluna litter is composed of four main components: woody material, long shoots, short shoots and floral parts that include seed capsules. Litter fall is almost negligible from young plants until the second or third growing season, hence the characteristic "bump" at the start of the growth curve shown in Fig. 14.19. Litter production increases until rates of about 200 to 250 g m⁻² yr⁻¹ are reached after about twenty years. Whilst some

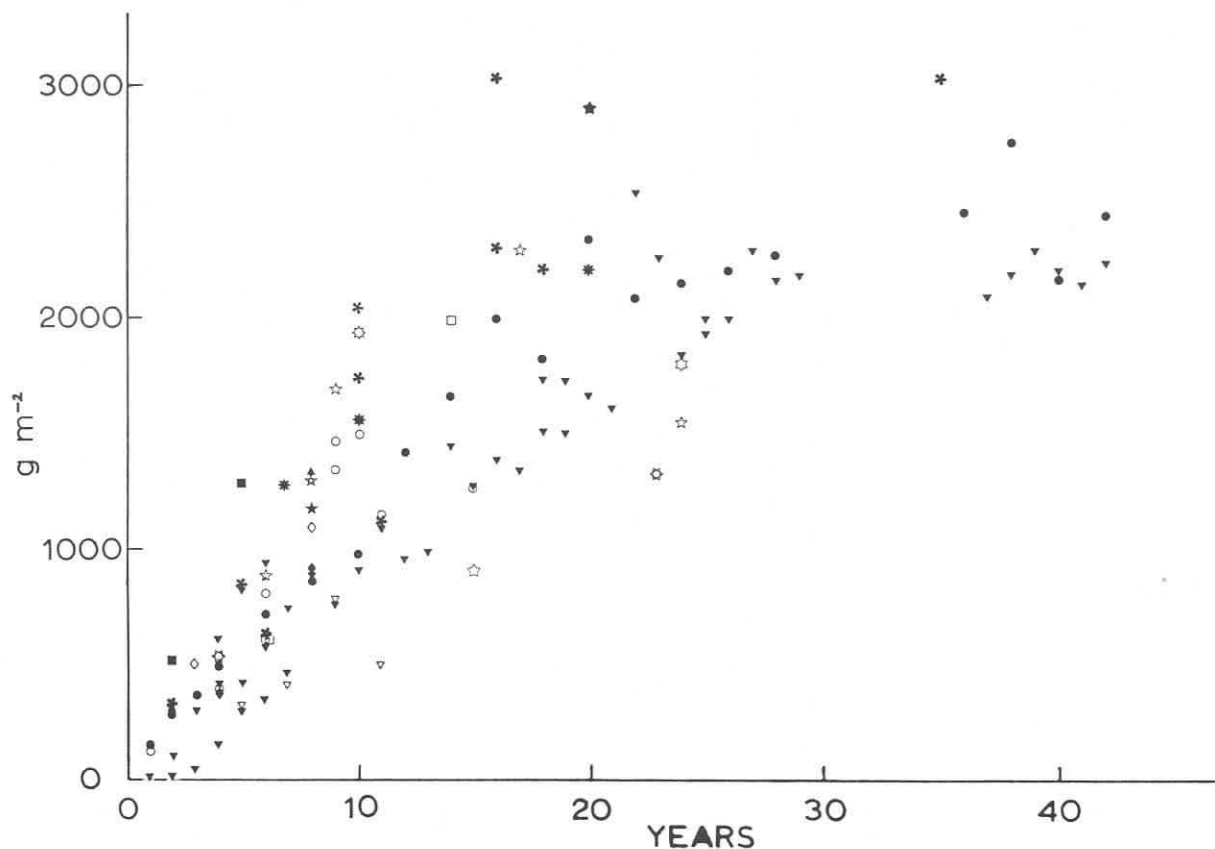


Fig. 14.20. Standing crop of European heathlands in relation to their age since the last fire. For symbols and sources of data see Table 14.7.

litter may be shed in all months of the year, there are two periods of higher fall. The first of these is in October and November due to the increase in short shoot material and the second in February (Cormack and Gimingham, 1964; Chapman et al., 1975a) when most seed capsules are shed. The work of Forrest (1971) on primary production by blanket bog vegetation at Moor House in the Pennines of northern England presents rather a different pattern where maximum shoot loss was between June and October. At that site snow cover effectively prevents litter fall during the winter months. Litter production by *Calluna* shows a good relationship with the above-ground standing crop (Fig. 14.23). The individual data obtained by different workers are shown in Fig. 14.23 with the relationship obtained from the smoothed data shown in Fig. 14.22; the latter suggest a more curvilinear relationship, due to the increase in the

relative amount of wood to shoot material in older heather.

Net above-ground primary production

A number of problems involved in trying to make comparisons between primary production of different heathland areas have been mentioned. These include variation with age, the differences in parameters measured by particular workers, and differences in their methods. Despite these problems there are four ways in which comparisons can be made.

(a) **Age.** It is unlikely that sufficient age sequences such as that published by Chapman et al. (1975a) (Fig. 14.24) will become available in the very near future to enable sites and areas to be compared in this way. Apart from the work involved, the

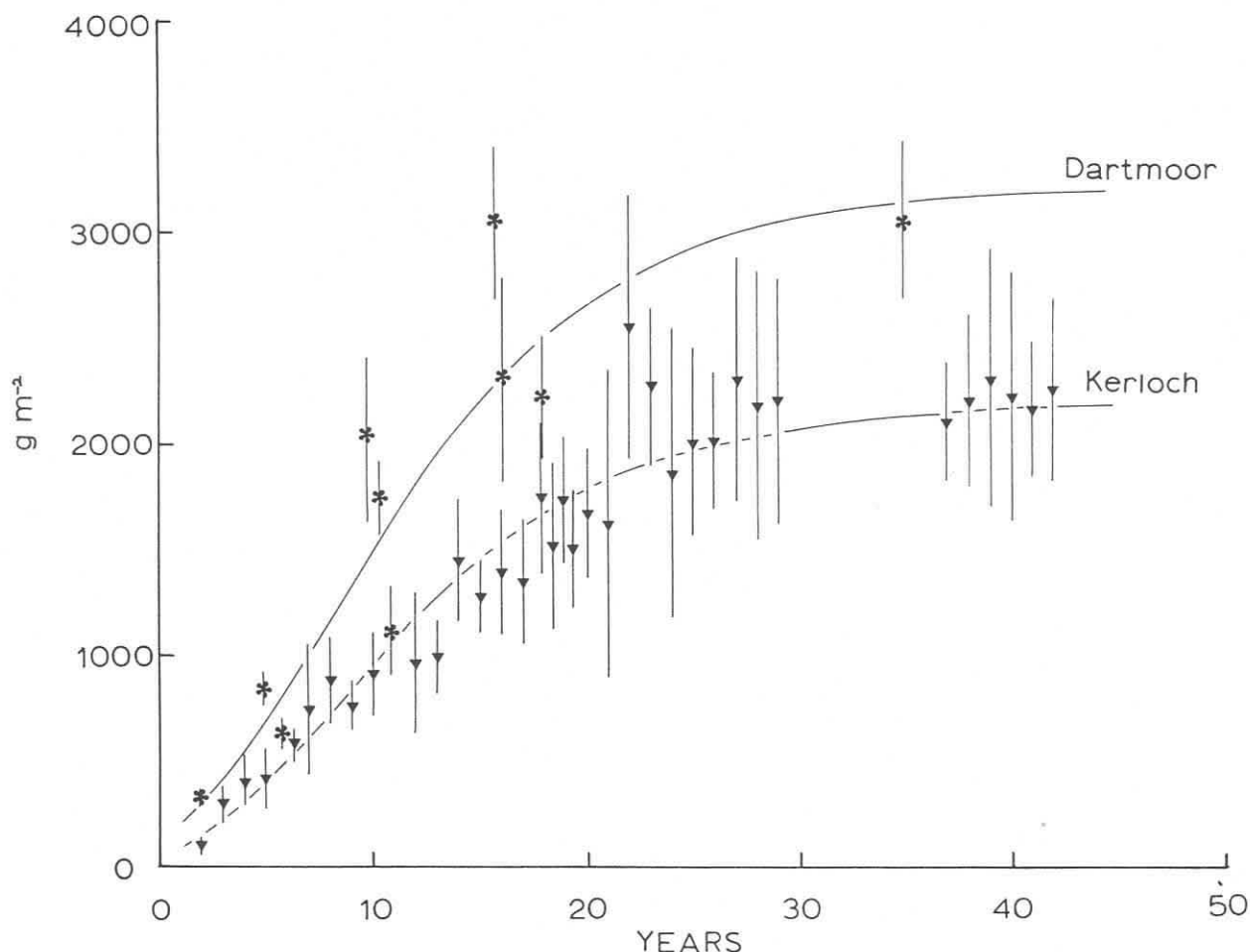


Fig. 14.21. Standing crop of above-ground vegetation from Dartmoor (Chapman, 1967, and unpubl.) and Kerloch Moor (G.R. Miller, pers comm.) in relation to age since the last fire.

scarcity of older stands makes this approach difficult. A more possible approach may be to make comparisons based upon some relative parameter that shows less variation with age than does total above-ground production. Relative production per unit weight of green material is such a parameter that might be worth considering. When calculated from the Dorset data relative production varies less with age than production expressed upon a simple ground-area basis. If relative estimates of production were based upon photosynthetic area, not easily measured in the case of *Calluna*, and allowance made for shoot age and interception of light by the heather canopy, an even less age-dependent parameter might be obtained.

(b) Developmental phases. The results obtained by different workers that can be designated to a particular developmental phase are summarised in Table 14.8. Despite the fact that some of the data relate only to shoot and flower production, a picture emerges where net above-ground production increases in the pioneer (or post-burn phase of Chapman and Webb, 1978), and the building phase, reaching a maximum in mature heather, and finally showing reduced values in the degenerate stage. The values reported by Barclay-Estrup (1970) are somewhat higher than those of other workers and are probably due to the fact that he was investigating shoot and flower production in the different developmental phases of a mixed-age site, and therefore sampled quadrats having

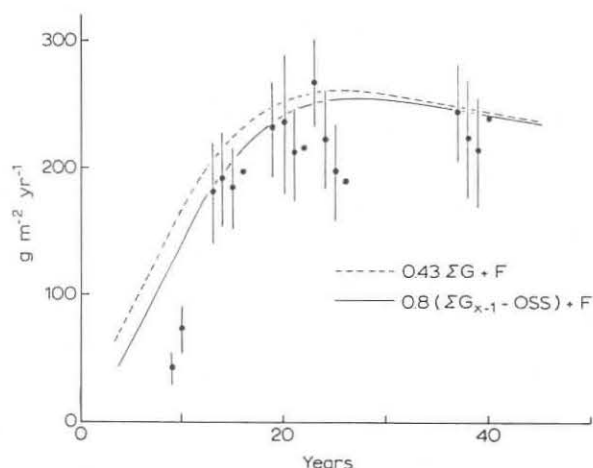


Fig. 14.22. Litter production by *Calluna* from Dorset heathlands in relation to their age. The point data ($\pm 95\%$ confidence limits) are from litter traps, the curves are indirect estimates of litter production (from Chapman et al., 1975a).

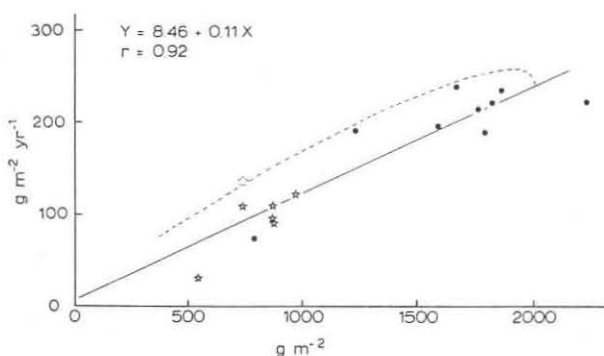


Fig. 14.23. Litter production by *Calluna* in relation to the above-ground standing crop. For symbols and sources of data see Table 14.7. The dotted line is derived from indirect estimates shown in Fig. 14.22.

particular physiognomic characteristics. In comparison with other workers who have sampled randomly within stands of a particular age his results might be expected to emphasise the features of a particular developmental phase, whilst those of the other workers provide more average values.

(c) **Corrected cover basis.** Miller and Watson (1978) have compared the estimates of flower and shoot production by *Calluna* that have been obtained by a number of workers in relation to altitude of the sites, after correcting the data to equivalent weights that would have been obtained

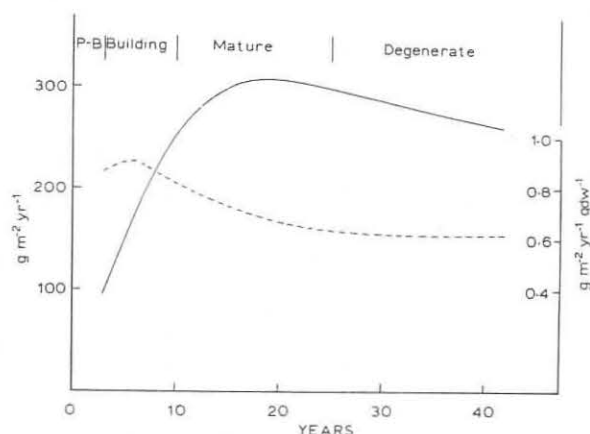


Fig. 14.24. Net above-ground production (solid line), and relative production (pecked line) of Dorset heathlands in relation to their age.

from 100% cover of *Calluna*. The information shown in Fig. 14.25 is based upon Miller and Watson's work, but with some additions and a consequently revised regression line. Comparisons based solely upon flower and shoot production must be treated with caution, as they may only reflect variations in the relative amounts of wood and shoot production. However, the production of green matter at Kerloch Moor (G.R. Miller, pers. comm.) and in Dorset (Chapman et al., 1975a) are very similar, as are the standing crop curves, so that it seems unlikely that such differences exist between these two sites.

(d) **Growing season.** A further way in which data can be standardised for comparison is by making allowance for the differences in growing season at different sites. This approach has been used by Summers (1972) and by Heal and Perkins (1976), but problems arise regarding the measurement and definition of the growing season, and more information is required before such an approach can be used with any degree of confidence.

Root production

In all discussions of primary production the question of root production arises, and very few data are available upon which any really meaningful statements or comparisons can be made. It must be remembered however that comparisons based solely upon above-ground estimates of net

TABLE 14.8

Above-ground production and standing crop data from some European heathlands according to the developmental phase of the vegetation

Site	Mean age (years)	Σ vegetation production (g m ⁻² yr ⁻¹)	<i>Calluna</i> production (g m ⁻²)	Σ standing crop (g m ⁻²)	<i>Calluna</i> standing crop (g m ⁻²)	Reference
Elsick Heath						
pioneer or post-burn	5.7	276*	149*	889	287	Barclay-Estrup (1970)
building	9.0	471*	442*	1702	1508	
mature	17.1	393*	364*	2305	1924	
degenerate	24.0	195*	141*	1561	1043	
Dorset Heathlands						
pioneer or post-burn	1.5	160	c. 90	291	—	derived from Chapman et al. (1975a)
building	6.75	230	193	811	573	
mature	17.5	323	298	1862	1502	
degenerate	32.5	298	278	2425	1966	
Skånör Heath, Sweden						
pioneer or post-burn	—	—	—	—	—	Tyler et al. (1973)
building	—	—	—	—	—	
mature	c. 15	307	232	920	741	
degenerate	—	—	—	—	—	
Moor House						
pioneer or post-burn	—	—	—	—	—	Forrest (1971)
building	8	407	168	1510	740	
mature	—	—	—	—	—	
degenerate	—	—	—	—	—	
Kerloch Moor						
pioneer or post-burn	4.5	—	168	—	420	Miller and Watson (1978)
building	13.5	—	210	—	1180	
mature	23.5	—	270	—	2000	
degenerate	39.5	—	239	—	2200	

* Shoot and flower production only.

production assume constant ratios of above- to below-ground production, and any preliminary conclusions made may well need modification when reliable estimates of root production become available.

Litter accumulation

Litter accumulation is the result of interaction between litter production and litter loss. The weights of plant litter accumulated at a number of different dry heathland sites are shown in Fig. 14.26. Whilst the scatter is considerable there is a clear correlation with the age of the site since burning, although there are insufficient data to

make any comparisons between sites, or between upland and lowland areas. While the combined data in Fig. 14.26 do not show any evidence of accumulation reaching a steady state, the results from Chapman et al. (1975b) on the Dorset heathlands that are shown in Fig. 14.27 indicate maximum values after about thirty years and do suggest an approach towards some form of steady state. On these heathlands it was shown that rates of decomposition derived from litter bags could be combined with estimates of litter production to predict levels of litter accumulation. When this was done the predictive curves (*A* and *B* in Fig. 14.27) are seen to differ significantly from the observed values. This discrepancy was explained by the

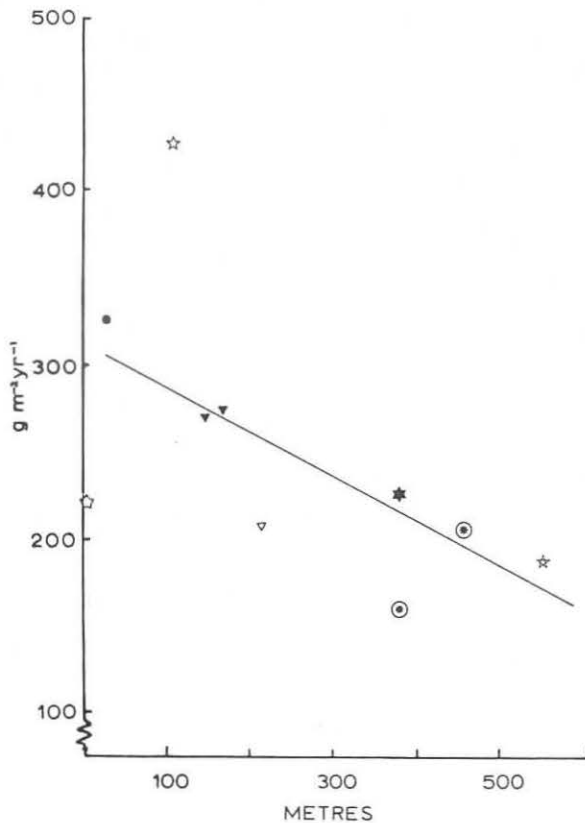


Fig. 14.25. Production of shoots and flowers by *Calluna* in relation to altitude (from Miller and Watson, 1978, with additions). For symbols and sources of data see Table 14.7.

invasion of the litter layer by roots once the vegetation had reached an age of about 10 years. From then onwards the proportion of recognisable root material increases until it reaches about 0.4 after forty years. The root invasion of the litter appears to be related to canopy closure and the consequent maintenance of higher and more constant humidity at the soil surface. This root development is accompanied by changes in the overall nutrient dynamics of the litter layer that take place from about twenty years onwards. Up to this time the accumulation of nutrients in the litter is about the same as the rate of nutrient supply by litter production, but from then the rate of nutrient accumulation decreases rapidly and nutrients are lost from the litter layer (Fig. 14.28). In the absence of reliable root production data it is difficult to interpret the results fully, but there are clearly important changes when nutrients held in the litter layer become available, with important

consequences for the overall nutrient régime of the vegetation.

Nutrient budgets

The cycling, sources, and losses of mineral nutrients in an ecosystem such as heathland, where they are in short supply, are of obvious importance to the management and maintenance of the habitat (these are discussed at length by Groves in Vol. B, Ch. 16). A number of studies have investigated the nutrient capital contained within various components of the heathland system (Thomas et al., 1945; Robertson and Davies, 1965; Chapman, 1967; Chapman, 1970; Tyler et al., 1973). Inputs to heathland and moorland systems in the form of precipitation have been described by various authors (Gorham, 1958; Allen et al., 1968; Gore, 1968).

Losses of nutrients that take place during heathland fires have been assessed by Allen (1964), Chapman (1967), and Evans and Allen (1971). The distribution and changes in the nutrient content of heathland soils after fires have been investigated by Allen et al. (1969) and by Hansen (1969). Losses from a Pennine moorland ecosystem were estimated from stream-flow analyses and other data by Crisp (1966). An overall nutrient budget for lowland heathland in southern England was constructed by Chapman (1967) who showed that, except for nitrogen and phosphorus, losses incurred during burning could be replenished by nutrient inputs from rainfall over a twelve-year period (see also Vol. B, Ch. 26, pp. 251–252 and Fig. 26.2). It is also possible that phosphorus may be replenished by rainfall, but when nutrient contents in precipitation are low they may merely represent local redistribution rather than true inputs to the system. For example dust, pollen grains etc. may be derived from closely adjacent vegetation so that unfiltered rain samples give inflated estimates of nutrient input, whereas filtered samples may well provide underestimates. The maintenance of nitrogen levels by fixation plants such as *Ulex* spp., and nutrient losses by leaching, need more study before complete nutrient balances can be assessed.

Breakdown and decomposition of litter

Litter is that material which has been shed by the aerial parts of the *Calluna* plants and which lies

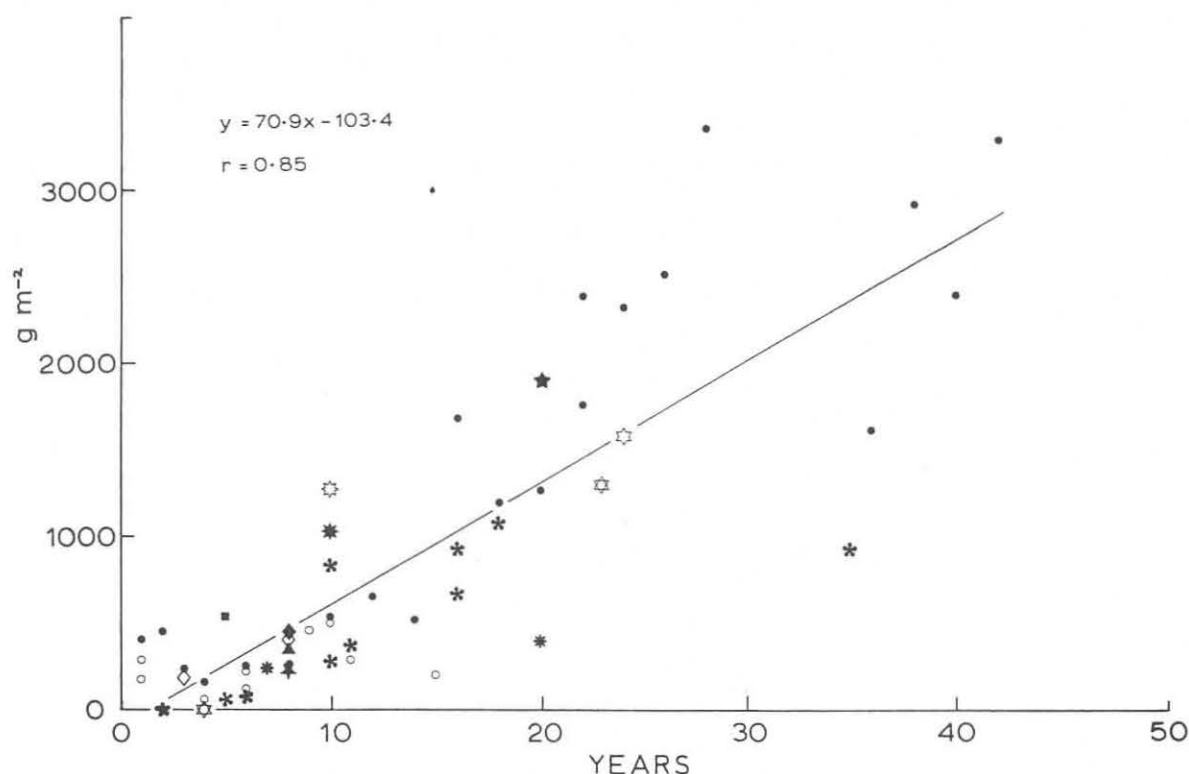


Fig. 14.26. Standing crop of accumulated litter on European heathlands in relation to the age of the vegetation since the last fire. For symbols and sources of data see Table 14.7.

upon the soil surface. Strictly speaking the plant also contributes to the litter with dead roots but the rate at which this occurs is difficult to measure, particularly on heathlands where the litter layer consists of an intimate mixture of fine living and dead roots as well as the dead aerial parts of the plant.

The phrase *litter breakdown* will be used to describe the physical changes which take place in the litter by the action of such factors as wind, water, frost and removal or comminution by animals, all of which cause the fragmentation of the material. *Decomposition* is the chemical degradation of the litter arising from the metabolic activity of soil organisms and causing its chemical simplification and the release of nutrients and energy. In many instances these two processes cannot be separated and are associated with physical movements of the litter; where this happens the term *litter loss* is more appropriate.

Table 14.9 gives the percentages per unit dry weight of the main nutrient elements in freshly fallen and accumulated *Calluna* litter, green

Calluna shoots and oak litter (Carlisle et al., 1966). Comparisons between the figures of Moss (1967, 1969) and of Chapman (1967) for green *Calluna* shoots and those for freshly beaten *Calluna* litter from plants in southern England (N.R. Webb, unpubl.) show that, on death, there is a drop in those nutrients that are readily leached, and a rise in the nitrogen content. Chapman et al. (1975b) give figures of 53.32% and 1.16% for the carbon and nitrogen contents, respectively, of brown short shoots (the main constituents of fresh litter), figures that suggest a C/N ratio of 46:1 for the newly fallen litter, a value indicating that it should decay readily.

The organic constituents of fresh *Calluna* litter together with comparative data for green heather shoots are presented in Table 14.10. The soluble carbohydrate content of fresh litter is 20% of that for the green shoots. This reduction in concentration may occur by leaching, utilisation of simple carbohydrates by leaf-surface fungi, or the withdrawal by the plant of carbohydrate for storage. Satchell and Lowe (1967) give values of 0.7

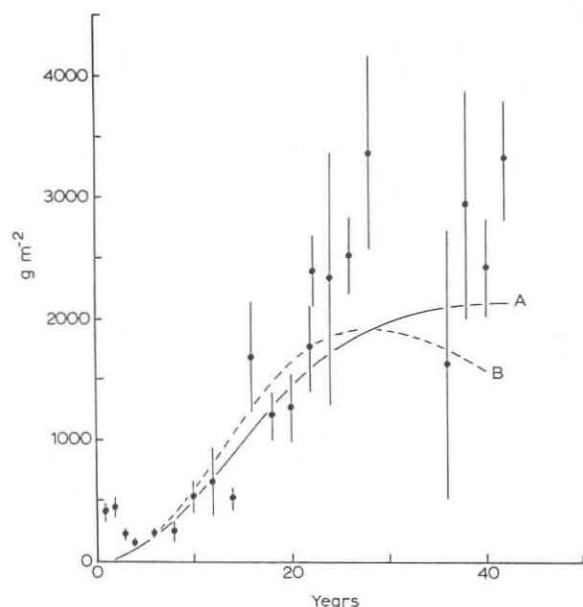


Fig. 14.27. The accumulation of organic matter in the litter layer of Dorset heathlands in relation to their age. Mean values ($\pm 95\%$ confidence limits) are from field data. Curves represent predicted accumulation from a constant decay rate (A) and from a linearly increasing rate (B). (From Chapman et al., 1975b).

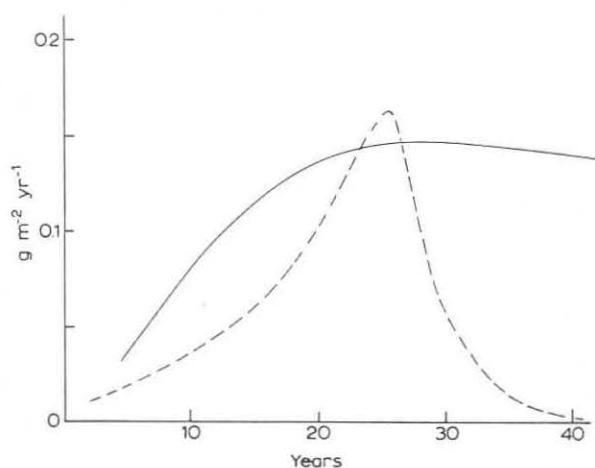


Fig. 14.28. The rates of accumulation (pecked line) and input of phosphorus (solid line) to the litter in relation to the age of the heathland since being burnt (based on Chapman et al., 1975b).

to 4.5% for the soluble carbohydrate content of ten species of temperate trees, and 0.7 to 2.0% for that of three coniferous species. The carbohydrate content of *Calluna* is higher than that of the conifers, and only exceeded by that of six of the trees. From this point of view *Calluna* litter, with a

fairly low soluble carbohydrate content, would not be the best substrate for organisms causing decay. Data are also available for the soluble tannin content of a similar range of litters. It has been shown that the content of polyphenols of plant litter affects its palatability to soil fauna (Heath and King, 1964; Satchell and Lowe, 1967). *Calluna* has a fairly high polyphenol content, which may explain its rather slow rate of breakdown and decomposition (Bell, 1974).

The commonest approach to studying the loss of *Calluna* litter has employed the litter-bag technique. A variety of *Calluna* litter types have been used in these experiments; Cormack and Gimingham (1964) used fresh litter, Chapman (1967) used the accumulated litter from the soil surface, and N.R. Webb (unpubl.) in Dorset has compared both fresh and accumulated litter. Only results from Moor House (Heal and Perkins, 1976) and Dorset have extended over several seasons; all other studies have been for one year. The results from Moor House and Dorset are similar, showing a weight loss of from 15 to 20% in the first year. At the Sands of Forvie, Cormack and Gimingham (1964) recorded rates between 6 and 15%. These weight losses are less than those of the litter in temperate deciduous woodland where Anderson (1973) found that up to 70% of the litter may have been lost after two seasons.

Litter-bag data are notoriously difficult to interpret. The presence of the bag considerably modifies the micro-environment of the decomposing litter (Anderson, 1973), but on heathland the main problem arises from an invasion of the bags by roots similar to that previously described for litter on the soil surface in the old phases. In Dorset up to 15% roots have been recorded in the litter in the bags after 2½ years. Root invasion may be stimulated by humidity changes and by the release of nutrients from the decaying litter. On Dorset heathland the bags are soon invaded by the litter fauna and within one season contain species similar to those in the adjacent litter.

Nutrient loss from litter bags on Dorset heathlands indicate losses of about 60% of the potassium and magnesium after four years, and 40% of the sodium, but hardly any loss of calcium and phosphorus. Indeed the concentration of phosphorus like that of nitrogen may even increase with time. There is almost no decrease over one year in

TABLE 14.9

Percentage (in dry matter) of the principal plant nutrients in *Calluna* and its litter

Type	Nutrient:	Na	K	Ca	Mg	P	N	C	Ash	C/N	Reference
Green <i>Calluna</i> shoots		0.047	0.43	0.40	0.16	0.081	1.18	—	3.51	—	Moss (1969)
Green <i>Calluna</i> shoots		0.056	0.44	0.68	0.24	0.083	1.28	53.3	—	41.6	Chapman et al. (1975b)
Fresh <i>Calluna</i> litter		0.031	0.104	0.52	0.081	0.071	1.09	—	4.05	—	Webb (unpubl.)
Accumulated <i>Calluna</i> litter		0.023	0.078	0.27	0.042	0.072	1.14	—	—	—	Webb (unpubl.)
Oak litter		0.029	0.095	0.69	0.11	0.055	1.04	51.3	3.30	49.8	Carlisle et al. (1966)

TABLE 14.10

Percentages (in dry matter) of the main organic components of *Calluna* litter and shoots

Organic constituent	Type:	Fresh <i>Calluna</i> litter	Green <i>Calluna</i> shoots
Soluble carbohydrate		2.7	13.3
Holocellulose		39.5	—
α -Cellulose		14.5	—
Soluble tannin		1.26	—
Crude fat		10.2	8.6
Lignin		35.6	—
Reference		Webb (unpubl.)	Moss (1969)

the soluble carbohydrate content, a decrease of 10 to 15% in both the holocellulose and α -cellulose contents, and less than 10% decrease in the soluble tannin content. From Table 14.9 it can be seen that much of the soluble carbohydrate content of short shoots of *Calluna* is lost before they fall as litter. The persistent tannin content, which is not reduced by weathering or decomposition probably renders the litter unpalatable to many organisms.

Densities of animal populations in soil and litter are smaller on heathland than in woodland. Their contribution to litter decay is likely to be small particularly since the larger species (earthworms and millipedes), which in woodland contribute significantly to breakdown of the litter (Raw, 1967; Satchell, 1967), are mostly absent. Chapman and Webb (1978) have estimated that cryptostigmatid mite populations of a square metre consume from 0.1 to 1.0 g dry weight of material each year, which represents about 1% of the annual litter fall; clearly the contribution of the litter fauna is small.

The microflora associations in peat beneath *Calluna* have been studied extensively (Heal and Perkins, 1976), but there have been few studies of microflora associated with *Calluna* on heathland.

Mangenot (1966) has shown from *in vitro* studies that *Calluna* and *Vaccinium* have leaves of a similar quality as substrates for micro-organisms. The succession of the microflora on decomposing *Calluna* leaves was followed but the flora was poorer than that associated with typical herbaceous types. Peptone- and pectin-decomposing yeasts were shown to be important in the decomposition of *Calluna* litter. However, a full study of the processes of decay and the involvement of micro-organisms of *Calluna* on heathland is required.

THE INVERTEBRATES

The invertebrate fauna of heathland has not received attention comparable with that of the floral components of the association. Until recent studies few attempts have been made to correlate changes in the fauna with the marked seral succession of the plants. Such changes can easily be seen from the pioneer or post-burn phases, in which the very open plant community has a poorer fauna, to the older, mature and degenerate phases which often have a rich and diverse fauna. As the growth cycle of the heather proceeds the spatial structure and the microclimate of the vegetation change, increasing the range of habitats which are available for exploitation by animals. At this stage the microclimatic changes should be considered since they have an over-riding influence on the development of the fauna.

On heathland, microclimatic studies have been carried out by Delany (1953), Stoutjesdijk (1959), Gimingham (1964), and Barclay-Estrup (1971), and the important aspect of temperatures, especially those occurring during heathland fires,

have been investigated by Whittaker (1961), Kenworthy (1963) and Webb (unpubl.). The results of Barclay-Estrup (1971) for a Scottish heathland show that the pioneer phase is characterised by extremes, especially of temperature. In this phase the humidity over the soil surface and beneath the plant is low, the plants are small and scattered and there is no litter layer. In some instances in a post-burn phase there may be a residual litter layer that has not been burnt by the fire, but this is soon dispersed by wind. In the pioneer and post-burn phases the habitats available for animals are few. Soil- and litter-dwelling forms are able to survive fires (Merrett 1976; Webb, unpubl.) since the litter layer acts as an effective insulator to the high temperatures reached in the vegetation (Whittaker, 1961; Webb, unpubl.). In the building phase conditions begin to stabilise, temperature fluctuations are less; as the canopy closes, the humidity beneath the plants begins to rise, and by this stage a litter layer has accumulated. Similar conditions prevail during the mature phase, but in the degenerate phase microclimate is more variable as the canopy opens. However, by this time the plants have reached considerable size, providing an important structural feature and protecting the litter layer.

Heather is a particularly difficult habitat to sample for invertebrates. Sweep-netting is difficult because of the woody nature of the vegetation and one of the most satisfactory methods is the vacuum sweep-net; however reliable density estimates are difficult to obtain from these methods. Likewise pitfall trapping is effective for recording the presence of surface active animals but it is completely unreliable in assessing relative numbers of species. Heat extraction of the soil and litter faunas usually provides reliable density estimates. It is however difficult to prescribe methods that are of value in assessing the faunas of heathlands and effective in measuring seral changes, and it is important to recognise that the efficiency of many sampling methods may vary from one growth phase to another because of changes in the structure of the vegetation. This may result in misleading impressions of changes, especially those of relative density, taking place in the fauna. The possibilities of using a wide range of methods have yet to be explored, and a manual such as Southwood (1966) should be consulted.

The earliest study of the insect fauna of heathland was that of Richards (1926) who, in an extensive survey of Oxshott Common, Surrey, recorded the insects found in a number of wet- and dry-heathland habitats, which represented the succession from burnt heathland to pine woodland. He came to the conclusion that there was a characteristic fauna associated with *Calluna* wherever it grew, and that the same fauna was associated with *Erica cinerea* and *E. tetralix*. It was Richards' view that the insect fauna was controlled by the plant rather than by any special edaphic or physiological conditions. The most important factors affecting the distribution of animals associated with *Calluna* were their powers of dispersal and their edaphic needs. A number of the species associated with *Calluna* were flightless, and as a consequence were absent from the early stages of colonisation. Richards noticed also that there were many species that occurred only in the older stands of *Calluna*, and that most of the insects found in the heather lived either beneath the plant or on the ground. It is this stratum of the habitat that is mostly highly developed in the older stands, accounting for the richer insect fauna.

The Studland Peninsula in Dorset was the site of an extensive ecological survey by Diver (Diver and Good, 1934; Merrett, 1971) from 1931 to 1939. This area contains salt marsh, dunes, dune slack, as well as dry-heathland, wet-heathland and bog. Diver was interested in the interactions between the plants and animals of this area, and in papers on Orthoptera (Diver and Diver, 1933), Syrphidae, Mollusca, Crambidae and Pyralidae (reviewed by Merrett, [1971]) he described the species present, their range tolerances with regard to factors such as wetness, vegetation structure, type of plant community and geology, and observations on the behaviour, especially that associated with feeding.

The next major study was that of Delany (1956) who examined the animal communities associated with pioneer heathland on three sites in the southwest of England. His study extended over fourteen months and was developed mainly as an adjunct to a study on the ecology of the thysanuran *Dilta littoralis*. He studied localities in the New Forest in Hampshire, the Pebble Bed Commons in south Devon, and on the island of Lundy in the Bristol Channel. He distinguished a mesofauna composed of animals which were over

5 mm in length, which he sampled by hand collecting from quadrats of 0.5 m², and a micro-fauna of animals under 5 cm in length which he sampled with a Tullgren funnel. He concluded that the mesofauna was made up mostly of species that occurred widely although there were a few that were associated only with heather. The Hemiptera had the greatest number of species associated with heather while the Coleoptera and Araneae had few species. Much the same picture emerged for the microfauna which he showed to consist of species which had a wide occurrence, especially the mites. Delany discussed his results in relation to those of Richards (1926), with which they were very similar. The mesofauna of pioneer heathland consisted mainly of species adapted to a wide range of habitats and it might be expected that, as the heathland matured, the number of species characteristic of this community type would increase. It is hardly surprising that the early colonisers of pioneer heathland were species of wide habitat tolerances.

Moore (1962), surveying the conservation problems of Dorset heathlands, used ten indicator species. One of each pair was restricted to heathland and the other was of widespread occurrence. He used the pair of dragonflies (Odonata) *Ceragrion tenellum*, restricted to heathland and bog pools, and *Pyrrhosoma nymphula* which occurs widely; and the butterflies (Lepidoptera) *Plebeius argus*, restricted to heathland, and *Eumenis semele* which is widespread. The ability of these indicator species to withstand changes in land use and to survive in isolated areas of heathland was assessed.

The heathlands of southeast Dorset have been the subject of intensive invertebrate studies emanating from Furzebrook Research Station. Studies have concentrated mainly on the patterns of distribution, changes in seasonal abundance, and recovery after fires, rather than on overall surveys. Brian (1964) and Brian et al. (1976) have made detailed investigations into the populations of ants (Hymenoptera: Formicidae), Merrett (1967, 1968, 1969 and 1976) has studied the spiders (Araneae), and Webb (in prep.) the soil fauna. Most of this work has been done in Dorset on Hartland Moor National Nature Reserve, almost the whole of which was burnt in 1959. It was two years later in 1961 that Brian commenced his study of the ants. A survey site of 8 ha, covering both

dry- and wet-heathland communities, was surveyed from 157 sampling points, at which records were made of thirteen species of ants present at sugar baits, altitude, soil moisture, soil organic matter and integrated soil temperature, the plant species present and the percentage of bare ground (Brian, 1964). All of the variables were highly correlated, and the data were subjected to principal component analysis. The four commonest species of ant were *Lasius alienus*, *Lasius niger*, *Tetramorium caespitum* and *Formica fusca*. The results indicated that *L. niger* inhabited the cool low wet areas, with plant cover of 83% composed mainly of grasses (*Molinia caerulea* and *Agrostis setacea*). The commonest heathland plants of this area were *Erica tetralix* and *Erica ciliaris*, and *Calluna* was present. Also living in this association were the ants *Myrmica scabrinodis* and *M. ruginodis*.

Formica fusca preferred the low but drier areas, although with a substantial amount of organic matter, and a vegetation cover of 85%, but in these habitats, which are similar to those of *Lasius niger*, *Calluna* was more abundant. The habitat of *Tetramorium caespitum* differed less than that of *Formica fusca* from *Lasius niger*. *Tetramorium caespitum* preferred the higher, warmer areas with a plant cover of about 62%. Grasses were less frequent and the vegetation consisted mainly of *Calluna* with some *Erica cinerea*. *Lasius alienus* lived on high, dry, warm and sparsely vegetated heathland with the lowest soil organic matter content. The interactions of the ants with the changes in vegetation are summarised in Fig. 14.29. This pattern of distribution on heathland has been tested experimentally by Elmes (1971), who transplanted whole colonies of *Lasius niger* into the habitats of *Tetramorium caespitum* and *Lasius alienus*. Elmes showed that colonies, transplanted as controls in other areas of wet-heathland and cool dry-heathland, survived well, but *L. niger* was unable to survive in regions typically occupied by *L. alienus*, and he considered these two sympatric species to be isolated by ecological as well as behavioural differences. This mechanism was reinforced in territorial selection by fertilised colony-founding queens.

Ten years after the first survey, Brian et al. (1976) surveyed the same area again in order to assess the changes in the ant populations. During this time the vegetation had developed through the post-

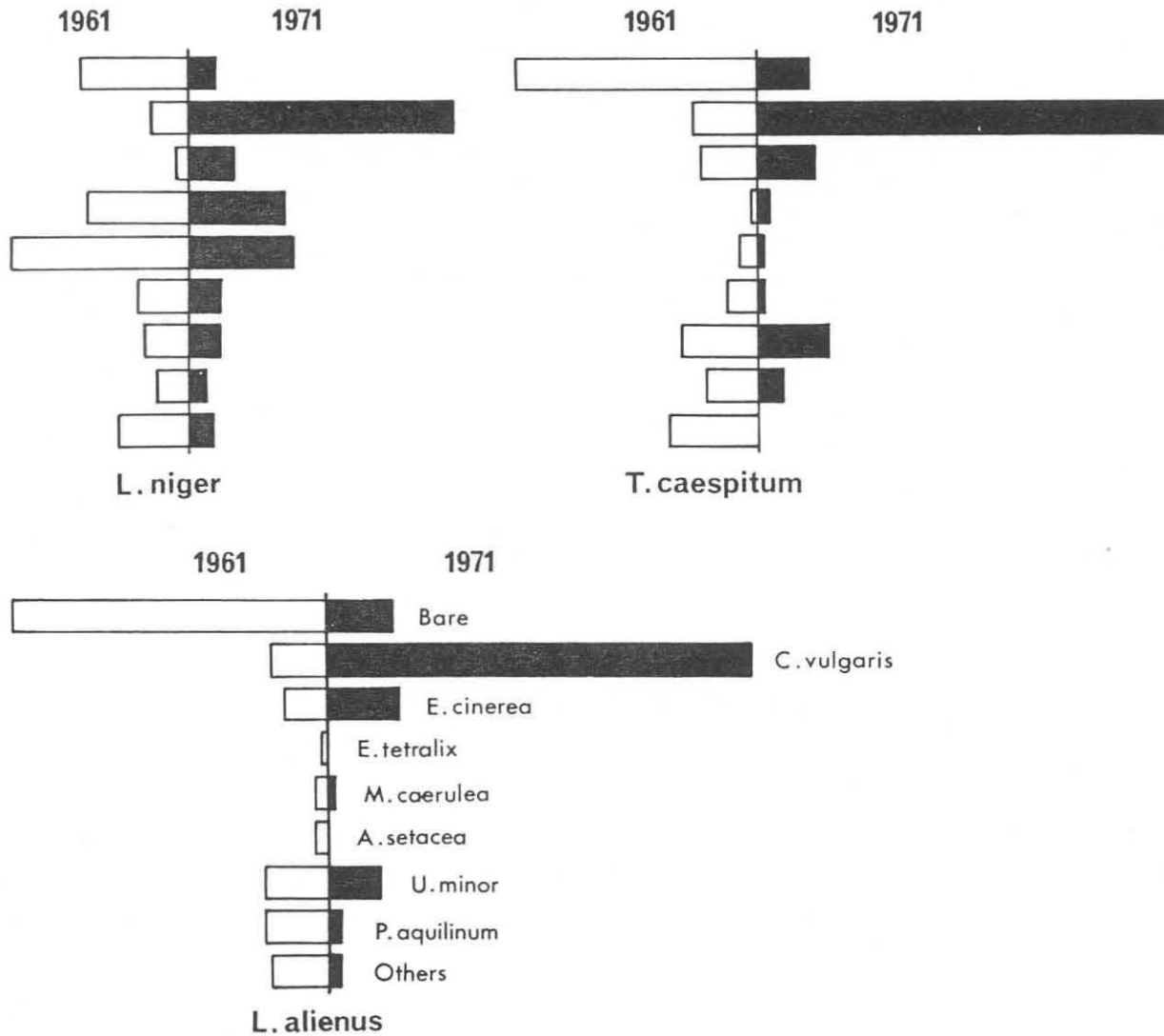


Fig. 14.29. The proportions of bare ground and components of the vegetation in areas inhabited by the three principal species of ants on a southern English heathland two years after burning and twelve years after burning (after Brian, 1964, and Brian et al., 1976).

burn phase to the late building phase. The most striking change was in the amount of bare ground which had decreased from 36% to 6%. *Calluna* cover had now increased from 10% to 54%, that of *Ulex minor* had hardly changed (10 to 11%) and species of *Erica* had become more common. Once again principal components were extracted in order to examine the distribution of ants in relation to features of soil and vegetation. The relative position that the ants occupied in the component space was similar to that ten years earlier. *Tetramorium caespitum* had increased from 17 to 24%

and *Formica fusca* from 6 to 15%, while *Lasius niger* and *L. alienus* had declined from 28% to 19% and from 42% to 24% respectively. *Formica fusca* had gained most at the expense of *Lasius alienus*. Brian et al. (1976) considered that the spread of the vegetation probably altered the competitive balance in favour of *Tetramorium caespitum* since this species is a seed feeder and can build nest mounds to avoid shading by the growing plants. Species such as *Lasius alienus* which require a high level of insolation decline as the vegetation spreads. Fire thus re-establishes a sparse plant cover which

is more suitable for *L. alienus*, and Brian et al. (1976) point out that these two species co-exist though being adapted to opposite phases of the burning cycle.

In a series of papers, Merrett (1967, 1968, 1969) has investigated, by continuous pitfall trapping for three years, the distribution and phenology of 195 species of spider on the same heathland. The changes which took place in populations of ground-living spiders following burning were described by Merrett (1976) from two adjacent areas, which were monitored continuously by pitfall traps for five years. Trapping was commenced in one area a week after it had been burnt, and at the same time in an adjacent area not subject to the burn. Both areas had been burnt five years previously, so that after five years' trapping results were available for the first ten years' growth of the heather. Vegetation and bare ground were recorded annually and the changes in the fauna correlated. The activity of the ground-living species was not markedly affected until the canopy closed and a litter layer started to build up at an age of about ten years. A total of 109 species were recorded, but only 51 of these occurred in sufficient numbers for analysis. Merrett was able to supplement these results with observations from other nearby sites. He recognised six categories:

(1) Pioneer species which declined in numbers quickly and which were absent when the plant cover had increased to 90%.

(2) Pioneer species which persisted ten years or more and showed a gradual decline in number over the ten years of sampling.

(3) Species which reached maximum numbers between five and ten years and whose numbers built up gradually over the ten years. Studies from other areas suggested that these species would decline in the 10-year to 15-year age classes.

(4) Species which reached peak numbers after ten years.

(5) Species typical of mature heathland and which were divided into two classes; web spinners, living mainly in the canopies of *Calluna* and *Ulex*, and ground-living species.

(6) Species whose period of peak abundance was uncertain.

The soil fauna of these heathlands has been examined by Webb (1972), Chapman and Webb (1978) and Webb (in prep.). Three sites were

examined by Webb (1972): degenerate heather which was at least thirty years old; mature heather fifteen years old; and building heather eight years old. A total of 35 species of oribatid mites (Cryptostigmata) were recorded but the numbers were similar from each of the sites — 26, 23 and 24 respectively. Most species occurred at all sites. Surprisingly, species of Phthiracaridae, which are usually associated with decaying wood and thus with the older stands, occurred in the younger stands, probably because they possess a thick exoskeleton protecting them from desiccation. There seemed to be little distinction between the number of detritus-feeding species and the number of fungal-feeding species. Differences, if any, are probably reflected in differences in the relative densities of the species. A later study (Webb, unpubl.) examined six sites which were respectively freshly burnt and 1, 4, 8, 15 and 27 years old since burning. In addition, the temperatures occurring in the litter and upper layers of the soil were recorded during experimental burning of heathland. The results were similar to those of Whittaker (1961) for a Scottish moor. The temperature recorded just beneath the litter surface was 65°C but at depths greater than 1 cm no temperature change could be detected, the fire passing over the surface too quickly. It seems likely that few soil and litter animals, except those at the surface, were killed during a heathland fire. The litter layers, as Whittaker (1961) and Whittaker and Gimingham (1962) have pointed out, possess extremely good insulating properties. The development of fauna closely follows that of the vegetation, and particularly the build-up of the litter layer. The litter remaining after a fire is gradually lost by the action of wind over the first three to four years after the fire. During this time the soil and litter fauna decline, with species of Phthiracaridae persisting the longest. The subsequent development of the fauna is slow and is impeded not only by the slow development of the litter layer but by its dryness. It is only when the mature phase is reached and the canopy closes that humidity rises and becomes more constant, and the fauna is able to develop.

Despite the extensive studies which have been described for the heathlands of southern Britain, no comprehensive survey of invertebrates has been undertaken which relates the distribution of the insects to the growth phases of *Calluna*. By contrast

the fauna of *Calluna*-dominated areas in the uplands of northern Britain have been well studied. But comparisons are difficult since not only the seral changes but the geographical differences in the distribution of the fauna have to be considered. Most of the southern heathlands lie within an area of particularly mild climate, and within the British distributions of many continental species at the northern limits of their ranges. Thus by comparison with the more northerly upland areas, the fauna of southern heathlands are rich and diverse.

At Moor House in the northern Pennines, extensive studies of the invertebrate fauna have been carried out over a number of years, latterly much of the work being under the auspices of the International Biological Programme. An early review of some of this work was made by Cragg (1961) and an extensive review has been compiled by Coulson and Whittaker (1978). It is not proposed to review this work further; it is strictly outside the scope of this chapter, since at this locality *Calluna* is mostly rooting in an organic and not a mineral soil.

At Scottish sites on a mineral soil, investigations have been carried out by Barclay-Estrup (1974) and Miller (1974). The study of Barclay-Estrup (1974) was essentially a preliminary one. Pitfall samples were analysed for a period of a little over a year. The greatest abundance of arthropods was in the degenerate and pioneer phases. In the latter case, the most abundant group was the ants, which prefer the higher levels of insolation afforded by the pioneer phase. Spiders declined initially after the pioneer phase but then numbers built up gradually towards a maximum in the degenerate phase. The myriapods by contrast are most abundant in the building and mature phases. Barclay-Estrup (1974) considered that the main microclimatic influence on the fauna was the humidity change associated with the closing of the canopy in the early building phase.

Miller (1974) made an extensive study of the invertebrates associated with the growth phases of *Calluna* on a Scottish moor. He investigated a mixed-age community representing all the growth phases of the heather and another which consisted of even-aged stands produced by burning management. At each of these sites he examined four habitats: the soil surface and within the litter; the litter surface; the canopy of the vegetation; and the

atmosphere above the canopy. The sampling methods involved pitfall trapping, sticky traps, heat extraction of soil and litter cores and vacuum sweep netting of the canopy. In addition features of the vegetation were measured to enable correlations with the animal populations to be made.

Miller (1974) concluded that in unmanaged heather of mixed age there was little change in either size or diversity of the invertebrate populations during the phases of the growth cycle. By contrast heather managed by burning and of an even age had population densities in the pioneer phase which were highest, and in which diversity was second highest. The greatest diversity was found in different phases depending on habitat. Burning resulted in lower diversity of faunas in the litter and the atmosphere above the plants, an increase in that on the litter surface and almost no change in the canopy. Thus, it would appear that, in a mixed-aged unmanaged *Calluna* community there is little difference between the faunas of the different phases, but in managed even-aged stands, although the composition of the fauna may be similar from phase to phase, densities are highest in the older phases.

These results are comparable with the results from the south of England, where the majority of heather communities are even-aged stands which have originated from a past history of management by burning. The pattern of faunal change in these stands is similar to that in Scotland. In general, the richest fauna occurs in the older, especially the late mature and degenerate, phases of the heather, which offer the greatest habitat diversity to the animals. It is only here that any characteristic heathland fauna can be recognised. The pioneer and post-burn phases, which last for about ten years, have an interesting fauna, composed mostly of colonising species and species which are adapted to conditions of bare ground or high levels of insolation, which disappears when the canopy closes. The subsequent fauna is more dependent on the equitable microclimatic conditions which become established in the older phases of the *Calluna*.

VERTEBRATE FAUNA

Herbivores

Vertebrate herbivores are not very numerous in European heathlands. This possibly reflects several of the special features of these heaths: their relatively recent origin, the low productivity of non-woody material, and the fact they have in many instances been systematically managed for the production of domestic herbivores. Mention has already been made of the pasturing of sheep and cattle (see p. 379): this section will deal briefly with naturally occurring herbivores.

Among mammals, perhaps the only one which is particularly characteristic of heathland is the mountain hare (alpine hare, blue hare), *Lepus timidus*. This species occupies upland and northern heathlands, often in considerable numbers, and is very largely dependent on *Calluna vulgaris* which in winter constitutes nearly 100% of its diet (Hewson, 1962). The density of mountain hares on upland heathlands varies considerably, ranging for example from few or none to as many as 38 per km² in spring. Densities above about 8 per km², however, are rare and seem to be associated with heathlands on soils of relatively high nutrient status with correspondingly enhanced concentrations of nutrients in the young, edible shoots of *Calluna*. It is noteworthy in this context that hares have been found to feed preferentially on *Calluna* which has been enriched by the addition of fertiliser (Miller, 1968).

The brown hare (*Lepus europaeus*) and the rabbit (*Oryctolagus cuniculus*) are to be found in lowland heaths, though both belong primarily to other types of vegetation and generally prefer grass and other herbage to *Calluna*. Rabbits, however, will graze *Calluna* intensively, particularly where it is close to their burrows (Farrow, 1917, 1925) and not too tall. Repeated grazing of young heather plants by rabbits causes very dense growth of new shoots and the development of compact, ball-shaped plants or a low spreading mat.

Red deer (*Cervus elaphus*) also make considerable use of *Calluna vulgaris*, although grazing and browsing on many other kinds of vegetation as well. Originally a forest animal, with the expansion of heathland and moorland in upland Britain red deer have become adapted to living in a largely

tree-less environment, normally seeking the shelter of woodland only in winter. They belong mainly to the high ground and to the wetter, western districts, rather than to *Calluna*-dominated dry-heathlands at low altitudes on the eastern side of the country, though they may spread into these in winter. Because of their importance for sport dating from about the middle of the nineteenth century, very large stocks were built up, often to the detriment of their grazing ranges and to neighbouring farms or plantations. Densities are still very high, compared to other parts of Western Europe, and deer stalking and shooting remains a valuable source of revenue to Highland estates. Promising experiments are also being conducted on deer "farming" in heathland areas of eastern Scotland.

Game birds constitute another group of heathland herbivores. In Scandinavia the willow grouse (*Lagopus lagopus*) is one of these, although not particularly closely associated with heathland. However, the British subspecies *Lagopus lagopus scoticus*, the red grouse, is pre-eminently a bird of heathlands (p. 379), feeding almost exclusively on *Calluna vulgaris* in winter. Even in summer *Calluna* usually accounts for over 50% of the diet, the remainder of which is composed largely of other heath species such as leaves and fruit of *Vaccinium myrtillus*, *Empetrum nigrum*, *Oxycoccus* spp., *Erica* spp., etc. Red grouse are territorial birds, the size of a breeding territory normally ranging from 2 to 5 ha (extremes 0.2 to 13.2 ha; Miller and Watson, 1974a). As with hares, the breeding stock of grouse varies in relation to the nutrient content of the edible shoots of their food plants, being greater in areas where the nutrient status of the soil is relatively high. On the poorer soils it can be shown that application of nitrogenous fertilisers increases the breeding stock of an area, and the same has been reported for phosphatic fertiliser on bog peat in western Ireland. There is also evidence that the density of grouse is related to the proportion of young stands of *Calluna* (2 to 3 years old, for instance when the concentration of nutrients in the shoots is high) in an area, so long as these are in relatively small patches, allowing the inclusion of both young and old *Calluna* in a territory (see Vol. B, Ch. 26). This relationship between population density and the area of young stands of *Calluna* is the prime reason for the management of "grouse moors" by burning (see Vol. B, Ch. 26).

Mountain and arctic heathlands support a related species, the ptarmigan (*Lagopus mutus*). *Calluna vulgaris*, where present, again provides a substantial proportion of the food of this species, but other plants are generally included according to availability, for example *Vaccinium myrtillus* and *Empetrum* spp. in Britain, or *Salix herbacea* in Iceland (Watson, 1964). Heathland bordering on forest provides a habitat for black grouse (*Lyrurus tetrix*), which ranges northwards from Belgium and The Netherlands to Scandinavia and Britain, as well as occurring in upland areas further south.

Estimates have been made by Miller and Watson (1974b) of the biomass, production and cropping of the most important herbivores on heathland in northeastern Scotland. Their figures are quoted in Table 14.11 as an indication of the low annual yield.

Insectivores

The rather numerous invertebrate fauna of heathland (pp. 401–406) attracts a variety of insectivores, few of which however occupy heathland exclusively or even preferentially. These include lizards (e.g. the viviparous lizard (*Lacerta vivipera*), common shrews (*Sorex araneus*) and in grassy areas wood mice and common voles (*Apodemus sylvaticus*, *Microtus agrestis*), and a variety of birds, notably the meadow pipit (*Anthus pratensis*), stonechat (*Saxicola torquata*) and wood-lark (*Lullula arborea*) among others. Frogs (*Rana*

temporaria) and newts (*Triturus vulgaris*) are encountered on wet-heathlands.

Some species, however, are particularly characteristic of lowland sandy heathlands. These include the sand lizard (*Lacerta agilis*), the smooth snake (*Coronella austriaca*) and the Dartford warbler (*Sylvia undata*), all becoming increasingly scarce as the habitats available to them disappear (Gimingham, Vol. B, Ch. 26). The Dartford warbler favours localities in which *Ulex europaeus* occurs abundantly amongst old *Calluna vulgaris*, a type of community generally resulting from a mosaic of not too frequent, small fires. It is a local resident on certain heathlands in southern England where its population has dwindled during the past century; allied races extend southwards from the Channel Islands and France.

Several ground-nesting species of birds move into open heathland for breeding, such as the curlew (*Numenius arquata*) and nightjar (*Caprimulgus europaeus*).

Predators

The larger herbivores of heathland have few predators. Foxes (*Vulpes vulpes*) and stoats (*Mustela erminea*) both feed on rabbits and hares as well as many of the smaller animals. Some of the birds of prey which hunt over heathlands and moors may sometimes take grouse or other game birds and their young; these include the hen harrier (*Circus cyaneus*), buzzard (*Buteo buteo*), and in the

TABLE 14.11

Estimates of biomass, production and cropping of four vertebrate herbivores on heathland in northwest Scotland

Crop	Average density in spring (number per ha)	Biomass (kg ha ⁻¹)	Production of young (number ha ⁻¹ yr ⁻¹)	Annual crop taken by man (number ha ⁻¹) (kg ha ⁻¹)	
Sheep	0.30	13.6	0.24	0.24	5.7
Red deer	0.089	6.1	0.015	0.014	1.1
Mountain hare	0.16	0.43	0.50	see note 1	
Red grouse	0.65	0.41	0.89		

Table from Miller and Watson (1974a), where references are given to primary sources of data.

These data are averages from a small number of study areas in northeast Scotland and so should not be interpreted too widely. For example, there are few sheep or hares in most of the Cairngorm Mountains.

¹ Mountain hares are seldom exploited and so it is impossible to calculate a reliable figure for the annual crop. However, data from a few moors where hares are particularly abundant and where bag records are kept suggest that an average annual yield of about 0.7 kg ha⁻¹ is obtained there.

more remote coastal or mountain districts the peregrine falcon (*Falcon peregrinus*) and golden eagle (*Aquila chrysaetos*).

The hooded crow (*Corvus cornix*) in the north of Scotland and northwards from The Netherlands and Belgium, and the carrion crow (*Corvus corone*) in the rest of the heathland region, will eat the eggs of ground-nesting birds including the grouse, as well as various small animals and carrion. Of these predators, the hen harrier is perhaps the most distinctly associated with heathlands, where it nests among *Calluna vulgaris*. A related species, Montagu's harrier (*Circus pygargus*), sometimes favours wet-heathland areas.

There are, in addition, various predators which take a variety of small mammals and birds. Adders (*Vipera berus*) may be very plentiful in heathland, both in dry sandy soils and also, to some extent, in wet heath. Wild cat (*Felis sylvestris*), in the more remote northern districts, hunt rabbits as well as smaller prey. Several hawks and owls include small mammals and birds, as well as insects, etc., in their diet: most typical of heathland are the merlin (*Falco columbarius*), the kestrel (*Falco tinnunculus*) and the short-eared owl (*Asio flammeus*), which hunts by day.

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